Feeding ecology of coral reef sponges

Dissertation zur Erlangung des Doktorgrades
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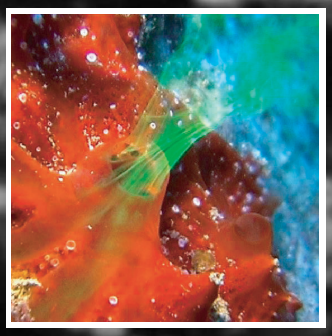

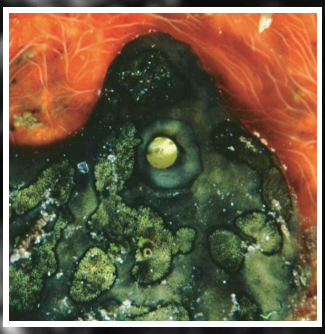
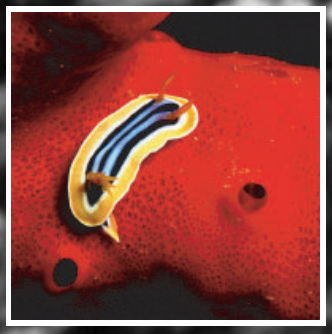


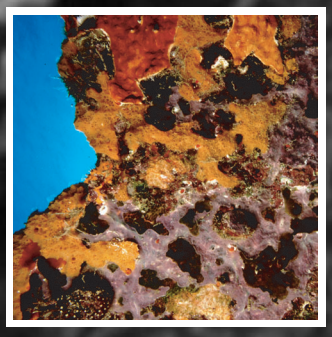
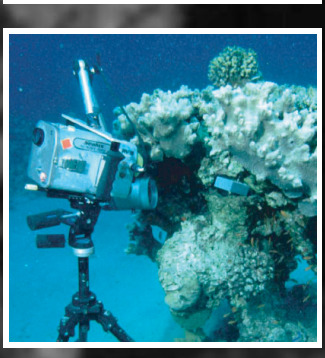

vorgelegt von

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Gutachter der Dissertation

1. Gutachter: Prof. Dr. Venugopalan Ittekkot
2. Gutachter: Prof. Dr. Gotthilf Hempel

Tag des öffentlichen Kolloquiums

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„Food is brought to them, waste is taken away. For them in their eternal abyss, with its time-like stream, there is no hurry, there is no return. Such an organism becomes a mere living screen between the used half of the universe and the unused half – a moment of active metabolism between the unknown future and the exhausted past.“

G. P. Bidder (1923) The relation of the form of a sponge to its currents.
Q J Microsc Sci 266:293-323

ACKNOWLEDGEMENTS

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Dear Mark, thank you so much for the last years, your love, help, support and encouragement !

ABSTRACT

Sponges are ubiquitous in coral reefs and in terms of biomass they are often second to corals. Inside coral reef crevices sponges are the dominant organisms, providing up to 60% of the living coelobite cover. We categorized them into 3 distinct groups according to their habitat: obligate coelobites (OC), living exclusively in coral reef crevices; facultative coelobites (FC), occurring both inside crevices and on the outer reef surface; and epi-reefal sponges (ER), dwelling only on the exposed reef surface.

In incubation experiments, cryptic sponges released 4 times more total inorganic nitrogen (TIN) (0.51±0.41µmol g $AFDM^{-1}$ h^{-1}) and 2 times more phosphate (0.07±0.05µmol g $AFDM^{-1}$ h^{-1}) than ER sponges. 72-91% of TIN released was in the form of ammonia, suggesting that coelobite mineralised nutrients are readily assimilable by algae and zooxanthellae in corals.

Comparative in situ measurements of ultraplankton uptake showed that retention efficiency differed between plankton groups: larger eukaryotic algae were retained less efficiently (~60%) than the smaller autotrophic prokaryotes *Prochlorococcus* and *Synechococccus* (>90%) with no marked differences between sponge groups. Heterotrophic bacteria were retained most efficiently by OC (83±6%, median±MAD), albeit at 8-fold lower pumping rates. Low volume throughput and high retention efficiency appear as adaptations of OC to the limited supply of plankton and low volume flow in framework crevices.

Molecular and histological techniques revealed that ER and FC sponges had only very low or moderate numbers of associated bacteria in their tissue whereas OC sponges harboured high densities.

OC and FC community uptake amounted to 0.60±0.36 g C d^{-1} per projected m^2 of reef, equivalent to one sixth of the gross productivity of the entire reef. ER community uptake was more than one order of magnitude lower, compounding the importance of coelobite filter feeders in harnessing pelagic material for the reef benthos.

PREFACE

This cumulative dissertation includes a summary, a general introduction and six articles. One of them is published, two are in press and two are submitted to international journals. This work has been supervised by Prof. Dr. Gotthilf Hempel and Dr. Claudio Richter. The field work for this study was conducted in the Caribbean and in Jordan as part of the Netherlands Bremen Oceanography Program (NEBROC) funded by the German Federal Ministry of Education and Research (grant no. 03F0218A/7) and the Red Sea Program for Marine Sciences (RSP)(BMBF, grant nos. 03F0151A and 03F0245A).

The articles are presented in the following chapters:

Chapter 1: C. Richter, M. Wunsch, M. Rasheed, **I. Kötter** and M. I. Badran
Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges
I shared the experimental field work with the first author, supplied crucial data on coelobite sponge biomass and was involved in the writing of the manuscript. This article was published in Nature 413, 18 th October 2001.

Chapter 2: **I. Kötter**, C. Richter, M.I. Badran and D. Marie
Mineralisation of ultraplankton by Red Sea filter feeders
This study was initiated and carried out primarily by myself. I evaluated the data and wrote the manuscript with editorial help of C. Richter. D. Marie performed flow-cytometry measurements and M.I. Badran supervised nutrient measurements. This article has been submitted to Marine Ecology Progress Series.

Chapter 3: M. Wunsch, S. M. Al-Moghrabi and **I. Kötter**
Communities of coral reef cavities in Jordan, Gulf of Aqaba (Red Sea)
The first author and I carried out the field work and wrote the manuscript. I evaluated the sponge community analysis resulting in the distinction of obligate and facultative cryptic sponge species. The article has been accepted

for publication in the Proceedings of the 9th International Coral Reef Symposium, Bali 2000.

Chapter 4: **I. Kötter**, C. Richter, M. Wunsch and D. Marie

In situ uptake of ultraplankton by Red Sea cavity-dwelling and epi-reefal sponges

This experimental study was initiated and carried out by myself. I wrote the manuscript with editorial help of C. Richter. M. Wunsch assisted in field experiments and D. Marie performed flow-cytometry counts. The article has been submitted to Limnology and Oceanography.

Chapter 5: **I. Kötter** and J. Pernthaler

***In situ* feeding rates of obligate and facultative coelobite (cavity-dwelling) sponges in a Caribbean coral reef**

This experimental study was initiated and carried out by myself. I evaluated the data and wrote the manuscript with editorial support of J. Pernthaler, who also helped with flow-cytometry measurements.

The article has been accepted for publication in the Proceedings of the 9th International Coral Reef Symposium, Bali 2000.

Chapter 6: **I. Kötter**, G. Schumann-Kindel, J. Reitner

Associated bacteria of coelobite and epi-reefal sponges in the Gulf of Aqaba, Red Sea

This study was initiated and carried out primarily by myself. G. Schumann-Kindel and J. Reitner provided support and advice with *in situ* hybridisation and microscopy. The material will form part of a note to be submitted to Marine Ecology Progress Series.

CONTENTS

ÜBERSICHT:

Schwämme — wichtige Planktonfilter und Nährstoffquellen im Korallenriff

Korallenriffe gehören zu den produktivsten marinen Lebensräumen. Sie beherbergen eine enorme Zahl unterschiedlicher Tier- und Pflanzenarten (Sorokin 1995). Das sie umgebende ozeanische Wasser ist dagegen sehr nährstoffarm, und die Konzentrationen der darin schwebenden tierischen und pflanzlichen Lebewelt (Zoo- und Phytoplankton) sind sehr gering (D'Elia 1977). Wie also schafft es das Korallenriff, sich und seine Bewohner unter solch kargen Bedingungen zu ernähren? Dieses so genannte „Korallenriff-Paradox“ beschäftigt Ökologen schon seit vielen Jahren (Odum 1971). Die Erklärung ist vielschichtig und fußt auf dem Zusammenwirken mehrerer Faktoren: Auch wenn die Planktonkonzentrationen im ozeanischen Wasser gering sind, so spült die Strömung immer neue Nahrung ins Riff (Erez 1990). Es kommt dabei also weniger auf die Konzentrationen an als auf die Stoffströme sowie auf die Fähigkeit der Rifforganismen, das eingetragene Material aufzunehmen. Starke Reduktionen in den Planktonkonzentrationen über dem Riff deuten auf eine gute Fähigkeit der Riffgemeinschaft hin, Plankton zu konsumieren (Glynn 1973, Bak et al. 1998, Yahel et al. 1998). Entscheidend sind die engen Nahrungsbeziehungen und Symbiosen innerhalb des Riffökosystems, die für eine mehrfache Verwertung des eingetragenen Materials sorgen und Verluste minimieren **(Box 1)**. Welche Organismen sind daran beteiligt? Wie funktioniert der "Planktonfilter Korallenriff" (Richter 1998)?

Box 1: Symbiosen und Recycling

Der wohl bekannteste Nährstoffkreislauf im Korallenriff ist die Symbiose zwischen Korallen und einzelligen Algen (Zooxanthellen). Die Algen ernten die Engergie des Sonnenlichtes durch Photosynthese und stellen die dabei entstehenden Zucker der Koralle zur Verfügung. Die Koralle wiederum gibt ihre Stoffwechselprodukte direkt an die in ihrem Gewebe lebenden Algen ab, die diese für ihr Wachstum benötigen. Diese Partnerschaft ist sehr effizient und findet sich auch z.B. in Seeanemonen und Riesenmuscheln.

Ein Recycling von Nährstoffen findet aber auch zwischen anderen Destruenten und Produzenten statt: Auf und in dem Riff lebende Mikro- und Makroalgen nehmen die ausgeschiedenen anorganischen Nährstoffe der vielen Weidegänger und Räuber gleich wieder auf – ein Grund, weshalb die Nährstoffkonzentrationen im Wasser so gering bleiben (Hatcher & Hatcher 1981). Dieser Zyklus ist aber nicht perfekt. Ständig werden auch gelöste Nährstoffe ausgewaschen und gehen dem Ökosystem verloren (Webb et al. 1975, Crossland et al. 1984, Smith 1984, D'Elia 1988) – ein Verlust, der nur durch erneuten Eintrag von außen kompensiert werden kann.

Zu dem ersten, grobmaschigen Filter gehören planktivore Fische und Korallen. Die tagaktiven Fische sind visuelle Jäger, die nach größeren Zooplanktern schnappen und in dichten Schwärmen als „wall of mouths“ regelrechte Planktonlöcher in die anströmenden Wassermassen fressen können (Hamner et al. 1988, Genin et al. 1994). Die Korallen, die sich

am Tage mit Hilfe ihrer symbiontischen Algen vorwiegend autotroph ernähren, strecken in der Nacht ihre nesselbewehrten Tentakeln aus, mit denen sie effizient Zooplankton fangen (Sebens et al. 1996). Fische und Korallen allein können 20-80% der Biomasse des heranströmenden Zooplanktons (20-500 µm) fressen (Glynn 1973, Hamner et al. 1988). Weitere Zooplanktonfänger sind Hydrozoen, Weichkorallen, Gorgonien, Seefedern, Seeanemonen und Fischlarven (Gili & Coma 1998, Ribes et al. 1998, Coma et al. 1999).

Den nächsten Filter bilden die auf dem Riff sitzenden Filtrierer: Polychaeten, Muscheln, Wurmschnecken, Schwämme, Ascidien und Bohrschwämme fressen vorwiegend kleineres Zooplankton und Phytoplankton. Filtrierer haben verschiedene Mechanismen entwickelt, um die im Meerwasser suspendierten Organismen und das partikuläre Material zu fangen. Ihre Nahrung kommt meist in geringen Konzentrationen vor und ist außerdem oft so klein (<2 µm), dass sie nicht individuell gefangen werden kann (Gili & Coma 1998). Deshalb filtern sie oft große Mengen ihres Umgebungswassers, um genügend Nahrung zu erhalten. Ein Schwamm kann z.B. in 4-24 s ein Wasservolumen filtern, das seinem Körpervolumen entspricht (Reiswig 1974, Savarese et al. 1997).

Unklar war bislang, wie die dritte Stufe, der Feinfilter, im Korallenriff funktioniert. Die Untersuchungen von Wunsch und Richter (Wunsch & Richter 1998, Richter & Wunsch 1999) legen nahe, dass hierfür Filtrierer verantwortlich sind, die in den kleinen Höhlen und Spalten

Box 2: Schwämme

Bisher sind ca. 7000 rezente Schwammarten beschrieben, von denen 96% marin sind. Schwämme kommen vom Flachwasser bis in die Tiefsee in allen geographischen Breiten vor, die Hälfte aller beschriebenen Arten leben in Korallenriffen (van Soest, pers. Mitt.). Die Anzahl der Arten wird für das Rote Meer momentan auf ca. 300 und für die Karibik auf ca. 800 geschätzt. Wegen ihrer versteckten Lebensweise sind noch längst nicht alle kryptischen Schwämme beschrieben, und es werden oft neue Arten gefunden (van Soest, pers. Mitt.). Schwämme sind oft nach Korallen die häufigsten Tiere im Riff (bezogen auf ihre Biomasse) (Reiswig 1973, Wilkinson & Trott 1985). Obwohl Schwämme als die primitivsten mehrzelligen Tiere angesehen werden, haben sie sehr erfolgreich verschiedene ökologische Nischen in Korallenriffen besetzen können. Als sessile Organismen können sie ihren einmal gewählten Standort nicht mehr verlassen. Andererseits sind sie extrem regenerationsfähig und haben sich in Experimenten aus mazeriertem Gewebe wieder zu vollständigen Schwämmen entwickelt (Kilian 1980).

Schwämme können eine Vielzahl anderer Organismen beherbergen: Bakterien (s. auch Box 4), Pilze, Krebse, Nematoden, Polychaeten, Seegurken, Schlangensterne, kleine Fische und sogar andere Schwämme (Duarte & Nalesso 1996, Kelly-Borges 1997, Magnino et al. 1999, Gherardi et al. 2001, Wilcox et al. 2002).

Schwämme spielen eine wichtige Rolle bei der Konstruktion wie auch der Zerstörung des Korallengesteins (Goreau & Hartmann 1963, Wilkinson 1983, McKenna 1998). Als Bioerodierer ätzen Bohrschwämme kleinste Plättchen aus dem Gestein, um sich in ihm geschützt zu entwickeln (Warburton 1958). Diese Löcher bieten auch eine Angriffsfläche für weitere biologische, chemische und physikalische Erosion (Neumann 1966, MacGeachy & Stearn 1976). In der Folge zerfällt der Stein immer mehr oder es bilden sich Höhlen. Andere Schwämme spielen wiederum eine Rolle beim Aufbau des Riffes, indem sie, zumindest vorübergehend, Sediment mit ihrem Gewebe binden und hier eine leichtere Bildung von Gestein (Diagenese) durch chemisches Verbacken stattfinden kann (Wulff & Buss 1979, Marshall 1983).

leben, die das Korallenriff durchsetzen. Diese für Taucher unzugänglichen Bereiche des Riffes, wurden erst kürzlich mit Hilfe neuer, am Zentrum für Marine Tropenökologie, Bremen, entwickelter endoskopischer Verfahren untersucht (Wunsch & Richter 1998). Das Labyrinth von Gängen und Spalten bietet einen bislang kaum untersuchten Lebensraum innerhalb des Riffsystems und beherbergt eine Vielzahl von verschiedenen Tiergruppen, unter denen die Schwämme dominieren **(Box 2)**. Es wird angenommen, dass Höhlen 30-75% des Gesamtvolumens des Riffes ausmachen (Ginsburg 1983, Kobluk & van Soest 1989) und den zur Verfügung stehenden Lebensraum durch ihre innere Oberfläche enorm vergrößern (Buss & Jackson 1979, Logan et al. 1984).

Wenngleich der Bedeckungsgrad dieser Höhlengemeinschaften und ihre Zusammensetzung für das Rote Meer inzwischen bekannt ist (Wunsch 1999) und die Dominanz von filtrierenden Organismen einen ursächlichen Zusammenhang mit den im Roten Meer und anderswo beobachteten Abnahmen von Phyto- und Bakterioplankton in Höhlen (Buss & Jackson 1981, Gast et al. 1998, Richter & Wunsch 1999) und über dem Riff (Glynn 1973, Ayukai 1995, Yahel et al. 1998) nahe legt, ist der Nachweis signifikanter Planktonzehrungen durch kryptische Filtrierer bislang nicht erbracht. Ebenso wenig ist bekannt, welchen Anteil die Aktivität höhlenbewohnender Filtrierer und assoziierter Mikroorganismen an der Mineralisierung allochthonen organischen Materials in den Spaltenräumen des Riffes hat und inwieweit dies zu den erhöhten Nährstoffkonzentrationen im Korallenstock beiträgt (DiSalvo 1971, Andrews & Müller 1983, Szmant-Froelich 1983).
Zur Beantwortung dieser Fragen fehlen bislang quantitative Daten über die Biomasse kryptischer Filtrierer und wichtige Informationen zur Ernährungsökologie, insbesondere der Filterleistungen, Nahrungspräferenzen und Exkretion. Diese Themen werden in den einzelnen Kapiteln dieser kumulativen Doktorarbeit behandelt.

Der Durchbruch für die Quantifizierung höhlenbewohnender Filtrierer gelang mit dem Einsatz endoskopischer Verfahren (LightSheet und CaveCam, Wunsch & Richter 1998, Wunsch 2000). Mit diesen Sonden konnten die Höhlenwände vermessen, die durch Organismen besiedelten Flächen bestimmt und deren Biomassen mittels Flächen-Gewichtsbeziehungen erstmalig quantitativ erfasst werden **(Kapitel 1).** Schwämme bedeckten mehr als 60% der von Höhlenfauna besiedelten Fläche. Bezogen auf die Riff-Fläche beträgt die Biomasse der Schwämme in den Höhlen 21 g C m^{-2}. Damit übertreffen die kryptischen Schwämme die auf der Riffaußenfläche um zwei Größenordnungen.

Durch gleichzeitige Messung des Wasseraustausches und der Veränderungen in den Chl *a* und Nährstoffkonzentrationen in den Höhlen gelang es, die Stoffaufnahme der Höhlengemeinschaft zu errechnen. Sie beträgt ungefähr 0,9 g C m^{-2} Riff Tag^{-1} – das entspricht fast einem Viertel des Gesamtumsatzes des Riffes.

Der direkte Nachweis, dass kryptische Schwämme und Ascidien Plankton aufnehmen und remineralisieren, wird in **Kapitel 2** erbracht. Schwämme filtrieren bekanntermaßen das Umgebungswasser, indem sie aktiv Wasser durch ihren Körper pumpen und dabei Partikel aufnehmen **(Box 3)**. Ein Großteil ihrer Nahrung besteht hierbei aus sehr kleinem (<2 µm) Picoplankton (Reiswig 1971 und 1990, Pile 1997, Pile et al. 1997), das effizient zurückgehalten werden kann (bis zu 99%, Reiswig 1971). Inwieweit kryptische Filtrierer vergleichbare oder - angesichts des geringen Partikelangebots in den Höhlen - gar höhere Filterleistungen aufweisen, war bisher nicht bekannt. Auch gibt es bislang noch keine Studien über das Nahrungsspektrum kryptischer Schwämme, oder den Einfluss der Wuchsform auf diese Parameter – kryptische Formen sind fast ausschließlich krustenbildend, freilebende oft massiv. Unterscheiden sich die Nahrungsspektren kryptischer Schwämme von Schwämmen, die auf dem Riff

Box 3: **Nahrungsaufnahme**

Das Wasser tritt durch zahlreiche Einstromöffnungen oder Ostia, die einen Durchmesser von 20-100 µm haben, in den Schwammkörper ein. Dann fließt es durch ein verästeltes System von sich verengenden Einstromkanälen (Riisgård et al. 1993), die in die Kragengeißelkammern (Choanocytenkammern) münden. Diese stellen die Basispumpeinheiten des Schwammes dar.

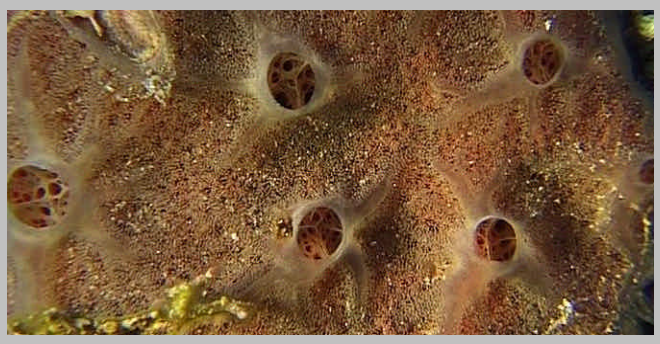

Abb. 1: Typischer Schwamm mit feinen Einstrom- und großen, runden Ausstromöffnungen

Jede Choanocytenkammer besteht aus 20-1400 Kragengeißelzellen (Choanocyten), von denen jede mit einer langen Geißel ausgestattet ist. Ein synchrones Schlagen aller Geißeln bewirkt einen gerichteten Wasserstrom durch die Choanocytenkammern, in denen Partikel bis zu einer minimalen Größe von 0,1 µm Durchmesser zurückgehalten werden. Die Nahrungspartikel werden an umliegende mobile Zellen weitergegeben, die sie verdauen und die Exkretionsprodukte an den Wänden der Ausstromkanäle abgeben. Nachdem das Wasser die Choanocyten passiert hat, fließt es in Ausstromkanälen weiter, die sich in der gleichen Weise wie die Einstromkanäle verzweigen. Diese vereinigen sich letztlich, und das gefilterte Wasser verlässt den Schwammkörper mit hoher Geschwindigkeit durch eine Ausstrompore (Osculum) (Abb. 2).

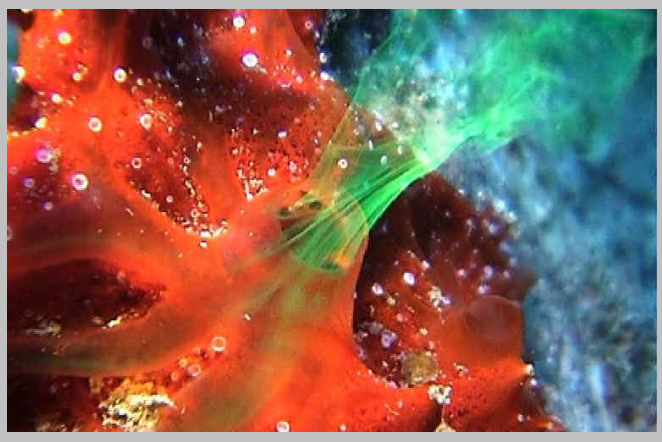

Abb. 2: Der grüne Farbstoff zeigt die Ausstromfahne

Hohe Strömungsgeschwindigkeiten des Ausstromwassers sind wichtig, um Refiltration zu vermeiden (Vogel 1994). Obwohl die Größe der einströmenden Partikel durch den Durchmesser der Ostia begrenzt ist, können Schwämme direkt an ihrer Oberfläche auch größere Partikel aufnehmen.

wachsen? Wie effizient erfassen sie verschiedene Größenklassen ihrer Nahrung? Beeinflussen unterschiedliche Wuchsformen (inkrustierend – massiv) die Nahrungsaufnahme quantitativ oder qualitativ? Wie viel der aufgenommenen Nahrung wird mineralisiert? Die Inkubationsexperimente, bei denen Ultraplankton in den für Höhlen charakteristischen niedrigen Konzentrationen angeboten wurde, zeigen, dass kryptische Schwämme mehr Plankton (<10 µm) aufnehmen als außen auf dem Riff wachsende Schwämme und Ascidien (**Farbtafel 1+2**). Ebenso mineralisieren sie einen größeren Anteil des assimilierten Planktons zu Phosphat und Ammonium, welches leicht von Algen und Korallen aufgenommen werden kann. Auch die Wuchsform hat einen Einfluss auf die Aufnahmeraten der Schwämme: Inkrustierend wachsende Arten können wesentlich mehr Plankton konsumieren als massive.

Die Analyse der kryptischen Schwammgemeinschaften in **Kapitel 3** führte zur Unterscheidung von obligat und fakultativ kryptischen Schwämmen. Erstere kommen ausschließlich in Höhlen vor, fakultativ kryptische Schwämme leben hingegen sowohl in kleinen Höhlen als auch in geschützten oder exponierten Bereichen der Riffoberfläche. Im Gegensatz dazu stehen die ausschließlich auf dem Riff wachsenden Schwämme.

Diese Gliederung in drei Klassen warf die Frage auf, ob es zwischen obligat und fakultativ kryptischen Schwämmen qualitative und quantitative Unterschiede in der Ernährung gibt. Inhärentes Problem einer kryptischen Lebensweise ist das knappe Futterangebot: Der Zustrom von Wasser in die Höhle ist nur schwach und die mitgeführte Partikelfracht nach Passage der verschiedenen Filterstufen äußerst gering (nur <30% des einströmenden Phytoplanktons erreichen die inneren Höhlenbereiche, Richter & Wunsch, 1999). Führte Nahrungslimitierung zu besonderen Anpassungen einer spezialisierten Schwammfauna - wie z.B. höhere Pumpleistungen oder besonders feine Filter? Oder überleben im Schutze der Spalten lediglich Arten, die durch Raubdruck und

Box 4: **Bakterien als Symbionten**

Es gibt eine Vielzahl von Symbiosen zwischen Schwämmen und Mikroalgen, Bakterien, Cyanobakterien (Wilkinson 1978, Corredor et al. 1988, Diaz 1997, Ritter et al. 2000) als auch unter Schwämmen (Rützler 1970, Wilcox et al. 2002). Die Biomasse mancher Schwämme besteht zu mehr als 50% aus Mikrosymbionten (sog. Bakteriospongien) (Reiswig 1981). Diese sind in zweifacher Weise wichtig: Zum einen nehmen Bakterien hauptsächlich gelöste Stoffe auf, während Schwämme überwiegend partikuläres Material verzehren. Zum anderen finden sich in Schwämmen auch photoautotrophe Cyanobakterien und vereinzelt auch Grünalgen, die – ähnlich wie die Zooxanthellen der Korallen – ihrem Wirt organische Stoffe liefern (Wilkinson 1979 und 1980). Manche Symbionten tragen sogar so viel zum Kohlenstoffbudget ihrer Wirte bei, dass diese als autotroph angesehen werden können (Wilkinson et al. 1988). Heterotrophe Bakterien sind vermutlich an der Speicherung organischer Moleküle und der Produktion sekundärer Metabolite beteiligt (Wilkinson & Garrone 1980).

Raumkonkurrenz vom exponierten Riff verdrängt wurden und nun am Rande ihrer physiologischen Möglichkeiten vegetieren? Zur Beantwortung dieser Fragen wurden obligat kryptische, fakultativ kryptische und exponiert lebende Schwämme vergleichend untersucht (**Kapitel 4**). Ein eigens entwickelter Probennehmer erlaubte, parallel das Einstrom- und das Ausstromwasser der nur 3 mm kleinen Oscula *in situ* zu beproben. Makroaufnahmen des Wasserstromes mit einer Videokamera gaben Aufschluss über die Geschwindigkeit des ausströmenden Wassers, und so konnten die Pumpraten der Individuen berechnet werden. Diese wiesen deutliche Unterschiede auf: Als Anpassung an niedrige Strömungsgeschwindigkeiten in den Höhlen haben obligat kryptische Arten wesentlich niedrigere Pumpraten als fakultativ kryptische und exponiert lebende Schwämme. Die Zusammensetzung des Ultraplanktons wurde, wie auch in Kapitel 2, mit Hilfe von Durchflusszytometrie analysiert. Sie machte deutlich, dass obligat kryptische Schwämme im Vergleich zu den beiden anderen Schwamm-Gruppen die kleinste Planktonfraktion (<1 µm) effizienter filtern können. Während exponiert lebende und fakultativ kryptische Schwämme durch eine höhere Pumpleistung auch eine höhere Aufnahme von Ultraplankton erreichen, würde diese Strategie bei obligat kryptischen Schwämmen zu Refiltration führen – sie maximieren stattdessen ihre Rückhalteeffizienz.

Die ersten vier Kapitel beziehen sich auf die Verhältnisse im oligotrophen Roten Meer, das sehr niedrige Plankton- und Nährstoffkonzentrationen (0,19-0,23 µg Chl *a* l^{-1}, Rasheed et al. 2002) im Jahresmittel aufweist. Doch wie verhalten sich kryptische Schwämme in nährstoffreicheren Meeren? Sind auch unter den mesotrophen Bedingungen der Karibik (0,2-0,8 µg Chl *a* l^{-1}, Gast 1998) nahrungsökologische Anpassungen wie in den Höhlen des Roten Meeres zu erwarten? Auch hier zeigt der Vergleich, dass obligat kryptische Schwämme viel weniger Plankton per Schwamm-Biomasse konsumieren als fakultativ kryptische **(Farbtafel 3, Kapitel 5)**.

Schwämme können mit einer Vielzahl von Symbionten zusammenleben **(Box 4)**. Am häufigsten sind Bakterien, die einen Beitrag zur Ernährung ihrer Wirte leisten können, indem sie gelöste organische Verbindungen (DOM) aufnehmen. Dies ist eine Fähigkeit, die für das Überleben in Gewässern mit niedrigen Konzentrationen von partikulärem organischen Material wichtig sein kann (Wilkinson & Garrone 1980). Eine große Dichte assoziierter Bakterien wäre möglicherweise ein Konkurrenzvorteil für kryptische Schwämme im planktonarmen Wasser

der Höhlen. Mit molekulargenetischen Fluoreszenzfärbungen wurde das Gewebe obligat und fakultativ kryptischer wie auch ausschließlich auf dem Riff lebender Schwämme auf assoziierte Bakterien untersucht **(Kapitel 6)**. Die ersten Ergebnisse bestätigen diese Vermutungen: In obligat und fakultativ kryptischen Schwämmen, die aus Höhlen stammen, finden sich sehr hohe Dichten von assoziierten Bakterien, während fakultativ und ausschließlich exponiert lebende Schwämme von der Riffaußenfläche nur mittlere oder geringe Dichten von Bakterien aufweisen.

ZUSAMMENFASSUNG UND SCHLUSSFOLGERUNGEN

Die allgegenwärtigen Höhlen und Spalten in jedem Korallenriff vergrößern dessen Oberfläche und bieten damit einen wichtigen, weitgehend geschützten Lebensraum für eine artenreiche Fauna. Die Morphologie der Höhlen kann sehr unterschiedlich sein: Im Roten Meer finden sich hauptsächlich schmale, tiefe Höhlen, während sie in der Karibik meist unter Korallenplatten oder zwischen massiven Korallenblöcken vorkommen und deshalb weit und flach sind. In beiden Höhlentypen sind jedoch Schwämme die dominierenden Organismen, mit einem Anteil von bis zu >60% an der von der Höhlenfauna bedeckten Fläche. Die Versuche, die im Rahmen dieser Arbeit durchgeführt wurden, zeigen, dass alle hier vorkommenden Schwammarten effektiv Phyto- und Bakterioplankton filtrieren. Sie machen durch Mineralisierung des partikulären und vermutlich auch gelösten organischen Materials (POM und DOM) den phototrophen Rifforganismen (Korallen und Algen) die Nährstoffe zugänglich, die diese für ihre Assimilation benötigen.

In Inkubationsversuchen, die durch Planktonabnahmen während der Versuchsdauer eine Verknappung des Planktonangebots in Riffhöhlen auf <30% der Freiwasserkonzentrationen simulieren, nehmen die kryptischen Schwämme mehr Ultraplankton auf als die auf dem Riff lebenden Schwämme und Ascidien. Darüber hinaus assimilieren sie mit Hilfe von assoziierten Bakterien vermutlich auch gelöste organische Stoffe, wie histologische Schnitte nahe legen. Sie scheinen damit an ihre POM-arme (und mutmaßlich DOM-reiche) Umgebung gut angepasst zu sein.

Inkrustierende Schwämme nehmen mehr Ultraplankton auf als massive Formen. Dies ist wahrscheinlich auf ihr höheres Verhältnis von Oberfläche zu Volumen zurückzuführen und

könnte zu der Erklärung beitragen, warum die meisten kryptischen Schwammarten in Form von flachen Krusten wachsen.

Eine umfassende Analyse der Aqaba-Schwammgemeinschaft ergab drei verschiedene Gruppen von Schwämmen: solche, die ausschließlich in Höhlen vorkommen (obligat kryptische Arten); Arten, die sowohl in Höhlen als auch exponiert auf dem Riff vorkommen (fakultativ kryptische Formen), und ausschließlich exponiert lebende Vertreter.

In-situ-Experimente zur potenziellen Aufnahmekapazität dieser drei Schwammgruppen unter Freiwasserkonzentrationen zeigen, dass fakultativ kryptische und exponiert lebende Schwämme das im Gegensatz zu den Höhlen 2-4fach höhere Nahrungsangebot mit bis zu 30-mal höheren Aufnahmeraten besser nutzen können als obligat kryptische Schwämme. Dies wird vor allem durch eine höhere Pumpleistung erreicht. Die äußerst geringen Pumpraten der obligat kryptischen Schwämme hingegen stellen vermutlich eine Anpassung an die nur schwache Strömung durch die Riffspalten dar: Starkes Pumpen wäre bei langsamem Plankton-Nachschub von Nachteil, da hier Pumpenergie in Refiltrierung gesteckt würde. So scheinen obligat kryptische Schwämme auf die doppelte Karte - hohe Filtereffizienz und geringe Pumpleistung - zu setzen. Darüber hinaus filtern die obligat kryptischen Schwämme die kleinsten Planktonpartikel – heterotrophe Bakterien – weitaus effizienter als die beiden anderen Formen. Eine Spezialisierung, die sich lohnt: Heterotrophe Bakterien können in riffnahen Gewässern bis zu 80% des Picoplanktons ausmachen. Mit nur <1 µm Durchmesser scheinen sie demgegenüber manchen Ascidien durch die Maschen zu gehen. Vermutlich nutzen Ascidien und Schwämme unterschiedliche Größenklassen der vorhandenen Nahrung und können deshalb auf engstem Raum nebeneinander existieren. In der Rückhalteeffizienz der übrigen Planktongruppen - autotrophe Cyanobakterien (>90%) und größere eukaryotischen Algen (ca. 60%) - weisen die Schwammgruppen hingegen keine Unterschiede auf.

Experimente mit obligat und fakultativ kryptischen Schwämmen in mesotrophen karibischen Gewässern untermauern die Ergebnisse, die im Roten Meer erarbeitet wurden: Auch hier nehmen obligat kryptische Schwämme wesentlich weniger Plankton auf als fakultativ kryptische, und dies obwohl die Höhlen, in denen sie leben, wesentlich offener und die Freiwasserkonzentrationen des Planktons höher sind.

Das von den Schwämmen aufgenommene Plankton wird zu leicht assimilierbarem Phosphat und Ammonium mineralisiert und kann damit direkt von den Primärproduzenten des Riffes (Algen und Korallen) verwendet werden.

Insgesamt zeigen die Ergebnisse, dass kryptische Schwämme als dominante Filtrierer eine Schlüsselrolle in der Versorgung des Korallenriffs mit neuen Nährstoffen spielen. Mit der Aufnahme sehr kleinen Planktons (und mutmaßlich auch gelösten organischen Materials) können diese Spezialisten ein Stoffangebot ausschöpfen, das anderen exponiert lebenden Rifforganismen unzugänglich bleibt. Ihr Eintrag von 0,6-0,9 g C m^{-2} Riff Tag^{-1} beträgt fast ein Viertel des Gesamtumsatzes des Korallenriffes.

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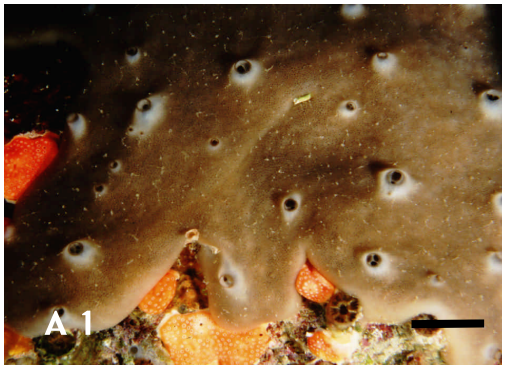

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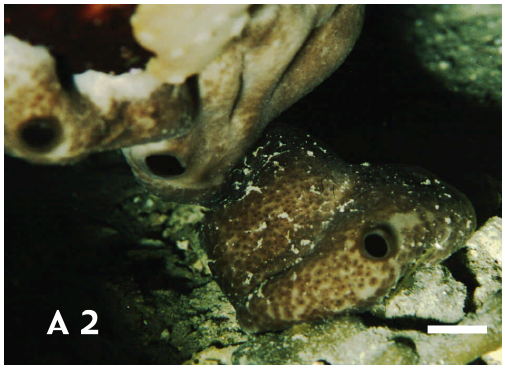

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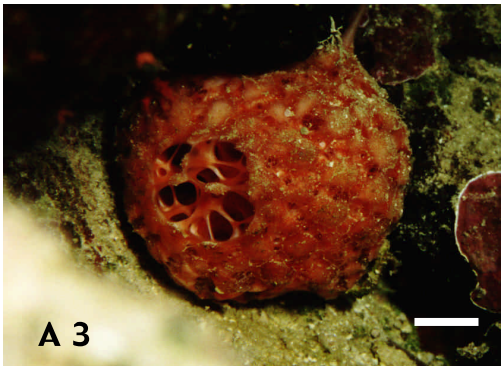

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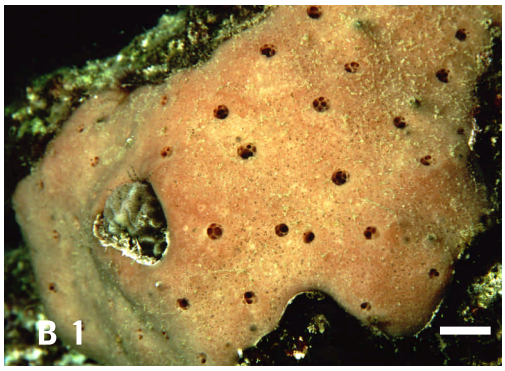
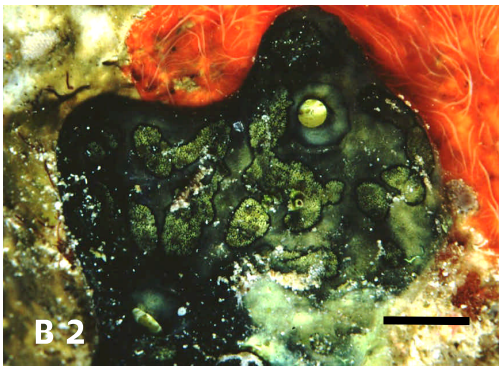
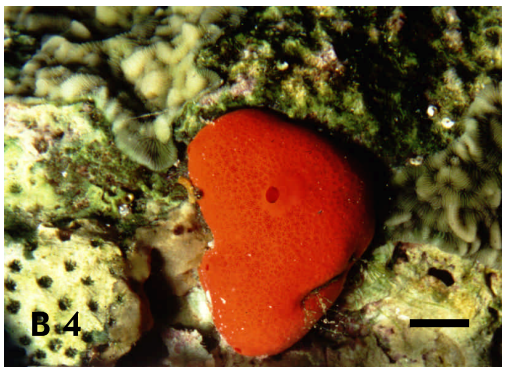


Callyspongia sp. 1

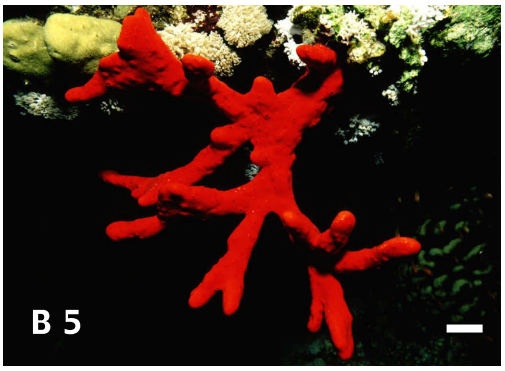


Hemimycale arabica

Monanchora sp.

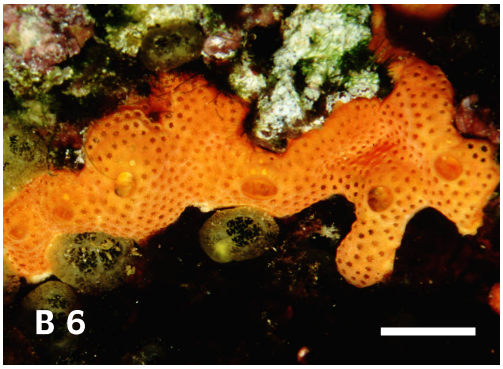


Negombata magnifica (inkrustierende Form)



Negombata magnifica (ästige Form)

Farbtafel 1: Untersuchte kryptische Schwämme in Aqaba, Rotes Meer
A1 - A3 obligat kryptische Arten, **B1 - B5** fakultativ kryptische Arten
(Maßbalken = 1cm)



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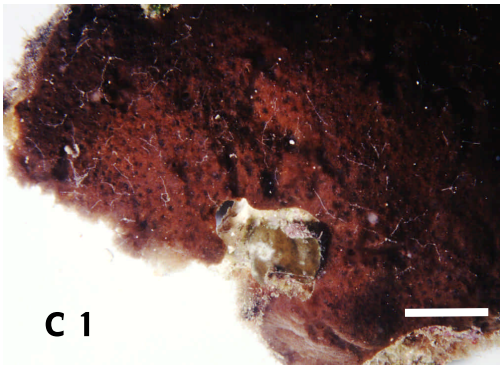

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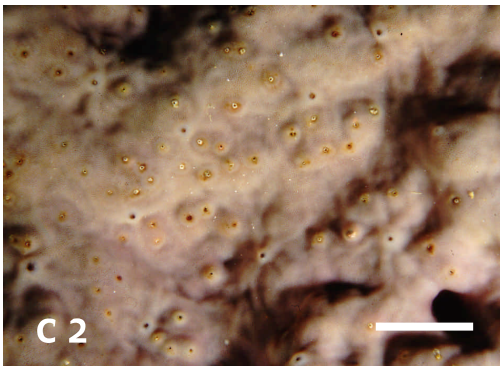
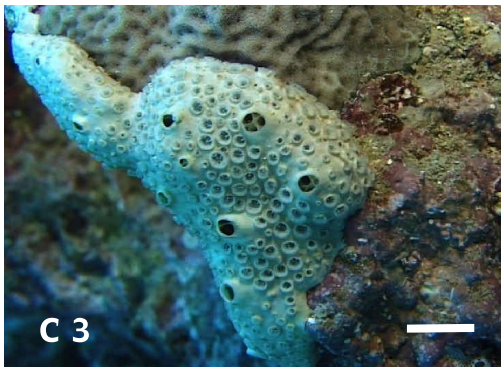


Chondrilla nucula



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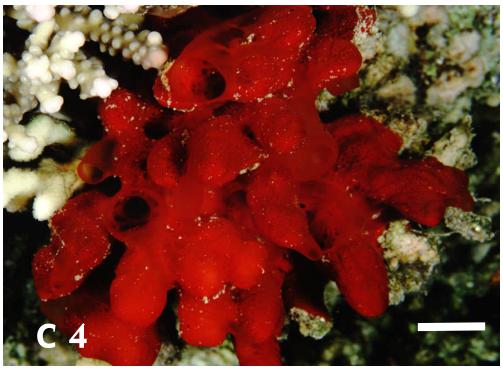
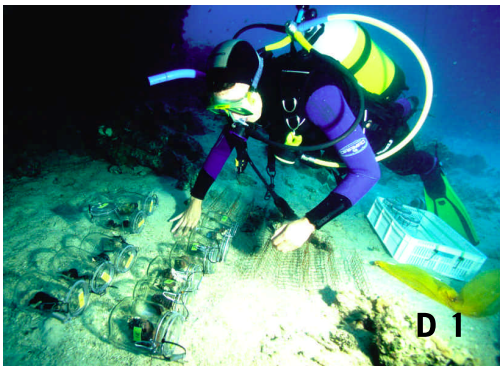
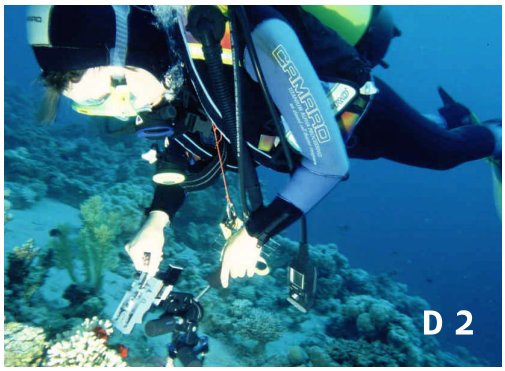


Mycale sp.

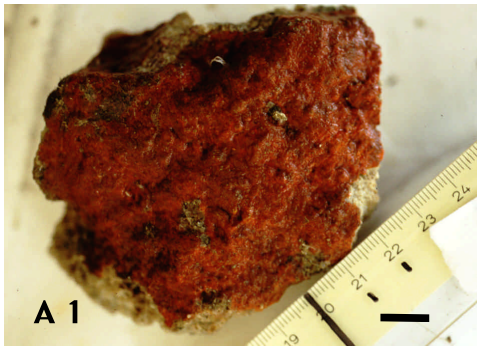


Inkubationsexperiment (Kapitel 2+5)

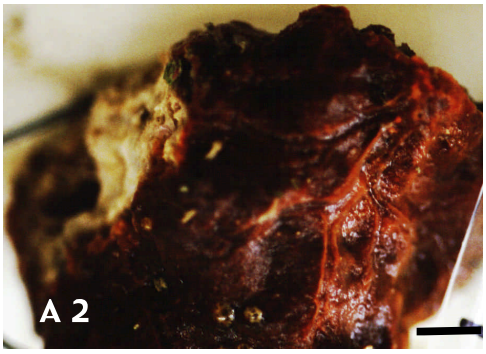


in situ Beprobung des Ein- und Ausstromwassers (Kapitel 4)

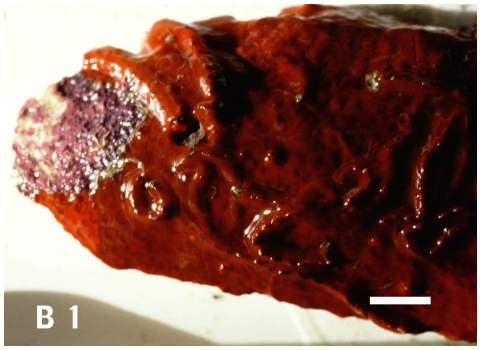
Farbtafel 2: Untersuchte Arten in Aqaba, Rotes Meer, und die Experimente
B6 kryptische Ascidie, **C1 - C4** ausschließlich auf dem Riff wachsende Schwämme, (Maßbalken= 1 cm) **D1 - D2** Versuchsanordnung



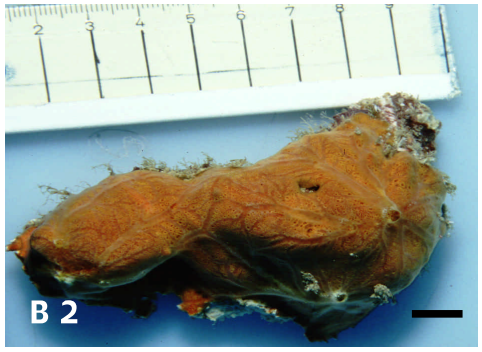
Desmanthus incrustans



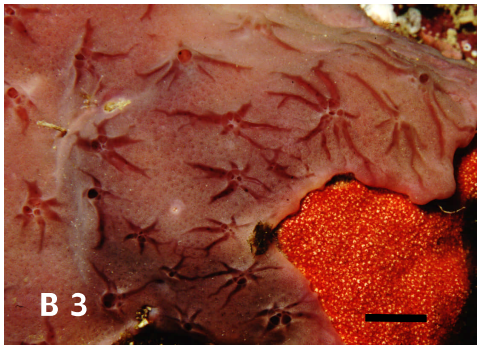
Diplastrella megastellata



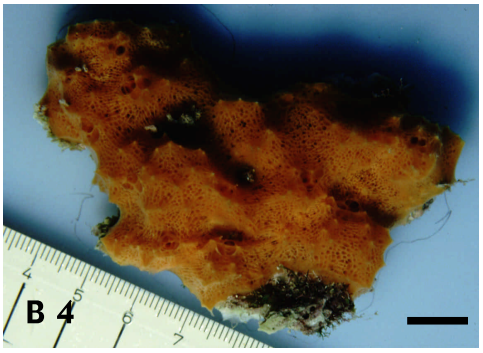
Merlia normani



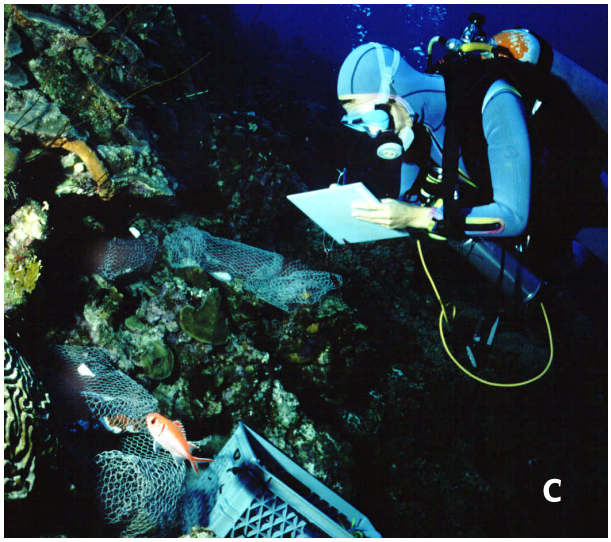
Clathria raraechelae



Halisarca caerula



Ulosa ruetzleri



Farbtafel 3: Untersuchte kryptische Schwammarten auf Curacao, Karibik
A1 - A2 obligat kryptische Arten
B1 - B4 fakultativ kryptische Arten, (Maßbalken= 1 cm)
C: Schwämme in Käfigen zum Schutz vor Fraßfeinden während ihrer Regeneration in 15 m Wassertiefe (Kapitel 2+5)

Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges

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Framework cavities are the largest but least explored coral reef habitat[1]. Previous dive studies of caverns, spaces below plate corals, rubble and artificial cavities[1–3] suggest that cavity-dwelling (coelobite) filter-feeders are important in the trophodynamics of reefs[2,4,5]. Quantitative community data are lacking, however, as the bulk of the narrow crevices interlacing the reef framework are inaccessible to conventional analysis methods[6]. Here we have developed endoscopic techniques to explore Red Sea framework crevices up to 4 m into the carbonate rock, revealing a large internal surface (2.5–7.4 m^2 per projected m^2 reef) dominated by encrusting filter-feeders. Sponges alone provided up to 60% of coelobite cover, outweighing epi-reefal filter-feeder biomass by two orders of magnitude. Coelobite community filtration removed more than 60% of the phytoplankton in the course of its less than 5-minute passage through the crevices, corresponding to an uptake of roughly 0.9 g carbon m^{-2} d^{-1}. Mineralization of the largely allochthonous organic material is a principal source of nutrients supporting coral and algal growth. The supply of new material by coelobites may provide a key to understanding the 'coral reef paradox'—a rich ecosystem thriving in nutrient-poor water.

Endoscopic estimates of crevice wall area and coelobite filter-feeder area cover were combined with field data on phytoplankton consumption and mineralization for the first comprehensive assessment of the role of coelobite filter-feeders in the coral reef nutrient balance. Research was carried out as part of the Arab/Israeli/German Red Sea Programme, providing access to various coral reefs in Egypt, Israel and Jordan (Fig. 1). The reefs as well as the characteristics of the study area have been studied in detail by various researchers (refs 5–11; and references therein). They represent typical flourishing Red Sea fringing reefs, characterized by a narrow shelf and a fairly open unconsolidated framework with little sediment infilling.

Line transects showed that 26–42% of the projected reef area is riddled by crevices of various sizes (Table 1, Fig. 2a). The median opening diameter of only 0.2 m renders these crevices inaccessible to visual inspection by divers using conventional methodology. We carried out detailed measurements of crevice dimensions with a diver-operated endoscopic video-camera (CaveCam[6]) combined with a radially projected light sheet mounted in front of the camera. This arrangement allowed us to outline the shape of the crevices in three dimensions and calculate their wall and cross-sectional areas (Fig. 3a–c; see Methods). Regression analysis showed a linear decrease in the ratio of wall to entrance area with cavity size (Fig. 2b). Combining these results with the line transect data yielded a cumulative coelobite living area of 2.5–7.4 m^2 of crevice wall per m^2 reef (Table 1). This is a conservative estimate considering the fact that many of the crevices extended beyond the range of the quantitative survey, and that the interconnections between anastomosing crevices[7] escaped detection by the light sheet.

We used the CaveCam in a different configuration with small headlights, a 45° mirror device, a close-up lens and spacers[6] to assess the corresponding community composition and living cover of coelobites (Fig. 3d). Quantitative analysis of 2,301 high-resolution images revealed a rich coelobite community covering 2.8 ± 0.9 m^2 per projected m^2 reef, excluding microfacies and sediment-covered areas. Coralline algae predominated near the sunlit entrances. Sponges abounded in posterior sections of the crevices, constituting 51–73% of the coelobite cover (Fig. 4a). The high densities, as well

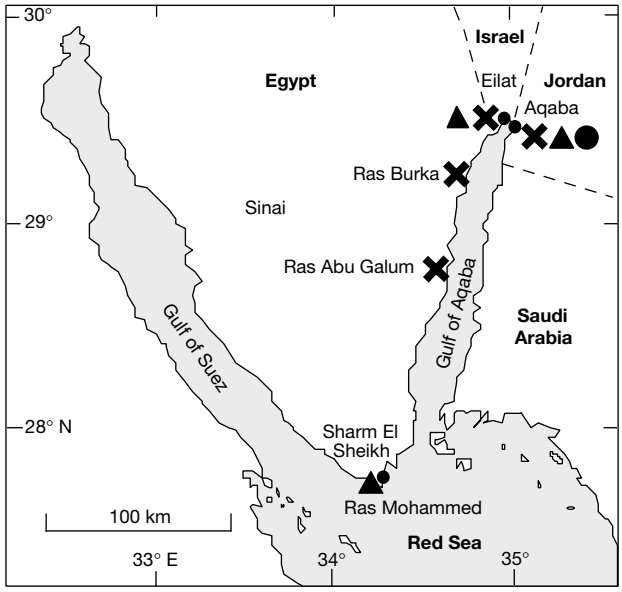

Figure 1 Map of the study area in the northern Red Sea and Gulf of Aqaba with sampling locations for crevice morphology and dimension, coelobite community and water exchange rates (triangles), Chl*a*, phaeopigments and oxygen (crosses), and nutrients (circles).

Table 1 Abundance and characteristics of framework crevice in Red Sea coral reefs

Transect no.	Study site	Transect depth (m)	Transect length (m)	No. of crevices per metre of reef	Metres of crevice per metre of reef	Crevice diameter (m)	s.e.	Maximum diameter (m)	Wall:entrance area	Wall area per projected m^2 reef
1	Aqaba	10	20	1.5	0.32	0.21	0.03	0.70	38.8	7.4
2	Aqaba	10	20	0.8	0.26	0.16	0.05	0.60	41.5	5.7
3	Aqaba	14	20	1.45	0.33	0.22	0.04	0.90	38.0	4.9
4	Aqaba	18	20	1.2	0.28	0.23	0.03	0.60	37.7	7.5
5	Ras Mohammed	3	50	1.1	0.42	0.39	0.05	1.80	31.0	4.0
6	Ras Mohammed	12	50	0.94	0.42	0.45	0.08	3.10	29.7	2.5
7	Ras Mohammed	12	50	1.14	0.38	0.33	0.06	2.30	35.0	3.0
8	Ras Mohammed	20	50	0.96	0.40	0.42	0.06	2.10	30.0	3.6
9	Ras Mohammed	20	50	1.14	0.37	0.33	0.04	1.50	33.9	3.8
All	Red Sea	3–20	20–50	1.14	0.35	0.33	0.02	3.10	35.1	4.7

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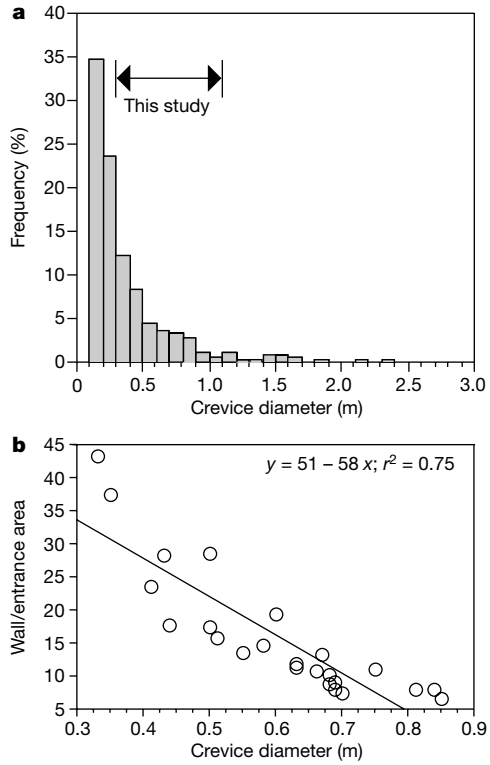

Figure 2 Physical dimensions of coral reef crevices. **a**, Length–frequency histograms of crevice opening diameters, showing the size range amenable to the endoscopic methods used in this study. Earlier studies by divers were limited to cavities with opening diameters much greater than 1 m, comprising less than 1% of the total number of crevices and much less than 1% of the total cavity area. **b**, Surface increase (ratio of crevice wall area to entrance area) as a function of cavity size, highlighting the importance of small crevices as living habitats in the coral reef framework.

as the dominance of delicate sheet-like growth forms (Fig. 3d), support the assumption that the distribution and abundance patterns of coral reef sponges are controlled by predators[12,13]. Less than 1% of the total area covered by sponges was due to erect or massive morphotypes, and less than 2% was due to boring taxa. Other filter-feeders (ascidians, bivalves, bryozoans and polychaetes) occurred regularly but at much lower densities, covering generally less than 5% of the substrate.

Qualitative wide-angle overviews with the CaveCam mounted on a flexible rod confirmed the pattern of well-flushed and densely populated crevices up to the 4 m reaches of the instrument. With a projected cover of 82 ± 55% per unit area of coral reef, coelobite sponges outweighed by far epibenthic sponges (0.2–1.2% cover[8–10]). Using an area : biomass conversion of 25.6 mg C per 10-cm^2 sponge, determined on small fragments of fresh reference material ($r^2 = 0.59$, $n = 25$), this translates into a coelobite sponge biomass of 21.1 ± 14.2 g C per m^2 coral reef (median ± MAD (median absolute deviation)).

Intense filtering by the coelobite community resulted in marked depletions of phytoplankton chlorophyll *a* (Chl*a*) towards the inner reaches of the crevices (64 ± 8% of the freestream waters; Fig. 4b; see Methods), alongside marked decreases in the ratio of Chl*a* to its degradation product phaeopigment (Fig. 4c). These findings are consistent with earlier measurements of bacteria and naked cell depletion in artificial cavities from the Caribbean[2]. Community respiration led to small but significant reductions in oxygen levels relative to freestream waters (5 ± 2%, Fig. 4d; Kruskal–Wallis test, $P < 0.0001$), reflecting the net heterotrophic nature of the cavity habitat.

Current speeds, determined by video-tracking of displaced particles and by dissolution of calibrated plaster cubes spaced over the length of the crevice, averaged between 0.9 and 5.5 cm s^{-1}. Wash-out experiments with fluorescent dyes featured half-life periods of only 75 ± 15 s, suggesting complete flushing of cavity waters within a few minutes.

Dye experiments showed that water flow through framework crevices was driven by flow speed differences across the bumpy reef surface, much like pressure-induced air flow through termite mounds, where the intake openings are located in troughs near the base and the exhaust openings in exposed position near the crest[14]. As a result, water flow was almost always directed into the crevices, leaving the framework through countless cracks and holes near the elevated parts of the reef.

The largely unidirectional flow pattern allowed us to determine the bulk filtering rate of the coelobite community using the standard flow respirometric approach[15]. Flux was calculated from the measured changes in Chl*a* and the rate of water exchange across a unit volume of cavernicolous reef, according to

$$F = \Delta\text{Chl}a \times rpk \quad (1)$$

where F is the amount of phytoplankton carbon filtered per unit volume of cavernicolous reef (g C per m^3 reef d^{-1}, or g C per m^2 reef d^{-1} normalized, for conservancy, to the upper first metre of framework); ΔChl*a* is the mean concentration difference between upstream and cavity waters (0.16 ± 0.01 mg Chl*a* per m^3 water; Table 2); r is a conservative value for the water exchange rate in the crevices (the inverse of the water residence time, as determined by fluorescent tracer experiments; 300 per day); p is a conservative value for the volume fraction of crevices per unit framework (0.3 m^3 water per m^3 reef; Table 1) and k is a carbon : Chl*a* conversion factor of 60 g C per g Chl*a* (ref. 10).

Table 2 Differences in chlorophyll *a*, phytoplankton biomass, total picoplankton and nutrient concentrations between cavity and freestream waters above the reef

	Measured					
	ΔChl *a* (μg l^{-1})	ΔNH_4^+ (μM)	ΔNO_2^- (μM)	ΔNO_3^- (μM)	ΔTIN (μM)	ΔPO_4^{3-} (μM)
Mean	–0.164	0.312	0.037	0.395	0.744	0.048
s.e.	0.014	0.097	0.003	0.043	0.116	0.008
n	32	64	64	64	64	64
P	<0.0001	0.1034	<0.0001	<0.0001	<0.0001	<0.0001
	Calculated					
	Phytoplankton (μg C l^{-1})	Picoplankton (μg C l^{-1})	New TIN (μM)	New PO_4^{3-} (μM)	New TIN (% of measured change)	New PO_4^{3-}
Mean	–9.84	–19.68	0.248	0.015	33.3	32.2

Picoplankton-derived new nutrients were calculated, assuming a conservative 1:1 biomass ratio between phytoplankton and other picoplankton (such as bacteria)[16] and stoichiometric conversion according to the Redfield ratio. Positive values denote enrichment, negative values denote depletion, relative to the freestream reference 2 m away from the reef. TIN, total inorganic nitrogen.

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Phytoplankton uptake by the coelobite community amounted to 0.89 ± 0.05 g C m^{-2} d^{-1}, equivalent to 22% of the gross community metabolism of the entire reef[15]. Total picoplankton removal, as suggested by the available biomass of bacteria in tropical waters[16], is probably more than twice this value, ranking our findings among the highest rates reported so far for marine and freshwater sponge communities[17,18]. This is corroborated by combining our biomass data (21.1 g sponge C m^{-2}) with reported food rations in benthic filter-feeders (2–10% body C d^{-1}; ref. 16), which yields similar values (0.4–2.1 g C m^{-2} d^{-1}).

Owing to the long doubling times of phytoplankton and bacteria (6–24 h; ref. 19) relative to the residence time of water over the narrow shelf (1–5 h; refs 5, 10), most of the picoplankton consumed in the reef originates from offshore, thus constituting a source of new material for the reef ecosystem.

Nutrient enrichments in the cavities suggest intense mineralization of the organic matter by the crevice biota (Table 2). Nutrient ratios near the Redfield ratio (N:P = 15.5; Table 2) reflect the

Figure 3 Endoscopic techniques for the study of crevice dimensions and coelobite communities. Wire-frame model of a framework crevice (Ras Mohammed, Egypt, 20 m depth) viewed from the side (**a**), front (**b**) and a 45° angle (**c**). Green circles, spaced 5 cm apart, mark reflection of a light sheet on crevice wall; yellow symbols mark the plumb line. **d**, Video close-up of coelobite community, including the beige sponge *Chondrilla sacciformis*, an unidentified yellow sponge (at right), solitary scleractinian polyps, the octocoral *Acabaria delicata* (below, left) and polychaete tubes (above, right). Position of the image in **d** is denoted by a square symbol in **a**–**c**.

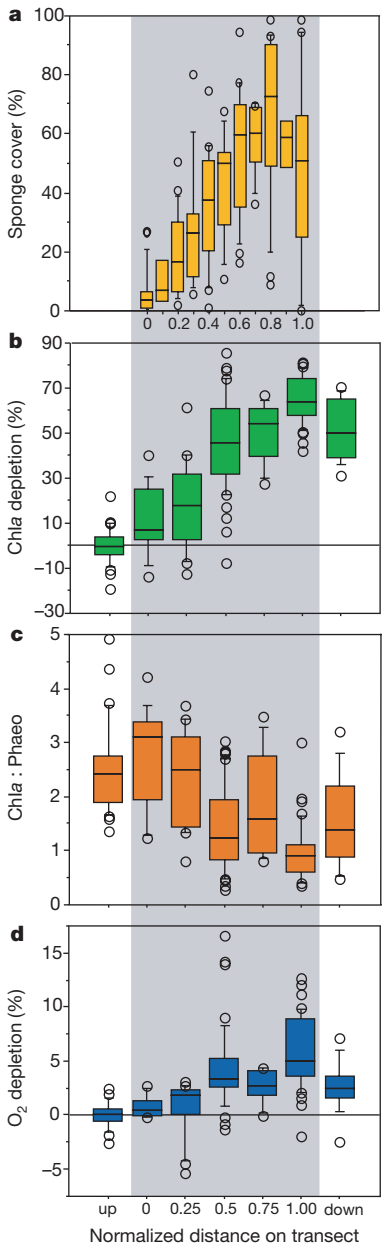

Figure 4 Small-scale distribution of coelobite sponges (**a**), Chl*a* (**b**), Chl*a*:phaeopigments (**c**) and oxygen (**d**) in Red Sea coral reef framework crevices, shown as composites of 25 (**a**) and 15 (**b**–**d**) surveys conducted within the study area (Fig. 1). Boxes and whiskers encompass 50% and 95% of the data, respectively; centre lines denote the median. In **a**, per cent cover is relative to total coelobite living area (2.8 ± 0.9 m^2 per projected m^2 reef). In **b**, **d**, depletions are relative to freestream waters (up) about 2 m above the reef. Downstream exits (down) of tunnel crevices show mixing with freestream waters.

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planktonic source of the mineralized material[16], contrasting the higher values reported for intrinsic reef material, for example in lagoonal patch reefs (N:P = 20; ref. 20), pore waters (N:P = 21; ref. 21) or benthic producers (N:P = 30; ref. 22). Stoichiometric conversion of picoplanktonic organic matter to inorganic nutrients (assuming 100% of the ingested food is respired) shows that allochthonous N and P may contribute one-third of the total nutrient flux emanating from the cavities (Table 2), in readily assimilable form (such as ammonia, 42% of N; Table 2) for corals and algae[16].

On the basis of the measured concentration differences and flushing rates, we estimate that 22.3 and 1.4 mmol m^{-2} d^{-1} of allochthonous N and P, respectively, are channelled into the coral reef system by coelobite filter-feeders, which exceeds the known import pathways through cross-shore advection of dissolved nutrients (1.9 and 0.3 mmol m^{-2} d^{-1}, respectively[23]), nitrogen fixation (0.6–1.0 mmol N m^{-2} d^{-1}; ref. 24) or migrating fish (2.4–7.2 mmol N m^{-2} d^{-1}; ref. 25).

The accrual of picoplankton by coelobite sponges and the associated enrichment of crevice waters with offshore nutrients may be a widespread phenomenon, as suggested by the occurrence of phyto- and bacterioplankton depletions near coral reefs throughout the tropics[4,5,10,26,27]. Our findings may therefore provide a general answer to Darwin's question[28] of how coral reefs manage to thrive in oligotrophic waters. □

Methods

Crevice numbers and sizes

We performed dive surveys to determine the total number and size distribution of crevices riddling the coral reef framework in Aqaba and Ras Mohammed (Fig. 1). Measuring tapes (50 m) were laid out at random, parallel to the 3-, 10-, 12- and 20-m depth lines (Table 1). Numbers and lengths of crevices intercepting the tape were recorded to the nearest 0.1 m.

Crevice morphology and dimensions

An endoscopic video system was used to assess the cross-sectional and wall area of 25 framework crevices in Aqaba, Eilat and Ras Mohammed (Fig. 1), at depths of 2–5 m (n = 9), 12–14 m (n = 8) and 19–20 m (n = 8). The system consisted of two parts: a camera head fitted with a 3-mm wide-angle lens, connected by a 3.8-m cable to its control (Panasonic KS-162) and video recording unit (Sony TRV-91E)[6]; and a modified 50-W halogen light mounted 60 cm in front of the lens, emitting a plane of light perpendicular to the axis of the camera. This configuration produced a highlighted contour at the intersection of the light sheet with the crevice wall. Moving the set-up in known increments (5 or 10 cm) on a rail along the axis of each crevice yielded a sequence of light rings outlining its shape in three dimensions (Fig. 3a–c). Video-images were digitized, and wall and cross-sectional areas were determined from the stack of scaled images for each crevice using Object-Image 1.62 software written by N. Vischer (ftp://simon.bio.uva.nl/pub). After correction of barrel distortion using Panorama Tools 1.7.2 by H. Dersch (http:// www.fh-furtwangen.de/~dersch), three dimensional wire-frame models of the crevices were obtained for visualization (Fig. 3a–c) using Rotater 3.5 by C. Kloeden (ftp://raru.adelaide.edu.au/ rotater/).

From the frontal aspect of a given framework crevice, it is obvious that the projected cross-section (Fig. 3b, white area around centre) is only a fraction of the cross-sectional area at the entrance. Given the limited air time underwater, it was not possible to customize the straight track of our system to the winding axis of each crevice, which limits the operational range of the quantitative surveys to 2.5 m. For consistency, the same margin was also applied to the quantitative investigation of the coelobite communities (below).

Coelobite cover

The CaveCam was used with a 7.5-mm close-up lens, 20-W headlights, a 45° mirror and spacers[6] to assess the corresponding community composition and living cover of coelobites. The walls of each of the 25 crevices were probed in 25-cm increments, taking sets of five 60×45-mm video frames of the sides, roof and bottom, respectively. The images were digitized and scaled, and the area covered by each taxon outlined manually with a digitizing pen for image analysis (NIH-Image; http://rsb.info.nih.gov/nih-image). Specimens were determined to the lowest taxonomic level possible and ground-truthed by taxonomic experts on the basis of reference material collected in the field.

Sponge biomass

Sponge material was obtained from small fragments of rock chiselled off the crevice walls. Tissue was scraped off the substrate using a dissecting knife. We obtained 25 samples of coelobite sponges ranging from 11 to 43 cm^2 in area cover for gravimetric determination of dry mass (24 h at 90 °C) and ash-free dry mass (AFDM; 5 h at 450 °C). Organic carbon was calculated using a C : AFDM conversion of 0.5 (ref. 16). Each specimen was photographed *in situ* before extraction to relate area cover (image analysis, above) to sponge biomass.

Currents and flushing

We determined water exchange through framework crevices by the dissolution over 24 h of plaster cards[29] spaced along the length of the crevices, and by short-term video-tracking of displaced particles using the CaveCam[6]. Additional dye experiments were carried out by injecting fluorescein into the centre of randomly selected cavities, halfway from the entrance, stirring, and measuring the decay of the fluorescence signal in syringe samples taken 0.5, 1, 2, 4, 8 and 16 min after initiation of the experiment. Regression of the log relative fluorescence versus time (seconds) yielded the relationship $y = 1.866 - 0.004t$ ($r^2 = 0.46$; n = 240).

Nutrients, oxygen and phytoplankton pigments

Triplicate samples for nutrient, oxygen and chlorophyll determinations were collected by an eight-channel peristaltic pump (Aqaba), which sampled simultaneously in crevice and freestream waters above the reef over a diel period alongside measurements of water exchange. Alternatively, samples were collected by divers (Fig. 1, other sites) drawing water through 100-μm screened silicone tubing into 100-ml polyethylene syringes. Intakes were spaced along the axis of crevices, and additional samples were collected from the downstream ends of tunnel cavities (Fig. 4, right). Cooled and shaded samples were processed within 2 h of collection. Oxygen was measured by Winkler titration[30], and Chl*a* and phaeopigments by fluorometry using the acidification method[30] (100-ml sample, 25-mm Whatman GF/F filters, 24 h of dark 90% acetone extraction at 4 °C). Filtrate ammonia, nitrite, nitrate and phosphate were determined spectrophotometrically[30].

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Mineralisation of ultraplankton by Red Sea filter feeders

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Abstract Sponges abound in Red Sea coral framework crevices. An *in situ* simulation study was carried out with seven species of cavity-dwelling (coelobite) sponges, two species of epi-reefal sponges and one ascidian to assess the role of active suspension feeders in the uptake and mineralisation of ultraplankton algae and bacteria. Coelobite sponges consumed more bacteria, prokaryotic and eukaryotic algae (54.2±47.4 µg C g ash-free dry mass [AFDM] $^{-1}$ h^{-1}) than epi-reefal sponges and about twice as much as the ascidian *Didemnum* sp. Coelobite sponges released four times more total inorganic nitrogen (TIN) and two times more phosphate than epi-reefal sponges (0.51±0.41 µmol g $AFDM^{-1}$ h^{-1} and 0.07±0.05 µmol g $AFDM^{-1}$ h^{-1}, respectively). 72-91% of TIN (total inorganic nitrogen) released was in the form of ammonia, suggesting that coelobite mineralised nutrients are readily assimilable by algae and zooxanthellae in corals. Our results provide mounting evidence that coelobite suspension feeders constitute a major source of nutrients supporting the high productivity of coral reefs in oligotrophic waters.

Keywords Coelobites, Suspension feeding, Coral reefs, Ultraplankton, Mineralisation, Sponges, Red Sea

Introduction

The recent application of endoscopic techniques (Wunsch & Richter 1998) to explore the maze of crevices interlacing the coral reef framework has unearthed a wealth of cryptic life (Richter et al. 2001, Wunsch et al. in press). High densities of coelobite (crevice-dwelling) sponges have been invoked to explain the enigmatic depletions of phytoplankton (Glynn 1973, Yahel et al. 1998, Richter & Wunsch 1999) and bacteria (Ayukai 1995, Gast et al. 1998, Scheffers et al. 2002) in near-reef waters, providing an important source of allochthonous nutrients to the reef primary producers (Corredor et al. 1988, Richter & Wunsch 1999, Richter et al. 2001). However, direct evidence for the contribution of coelobite filter feeders to nutrient cycling in coral reefs is still wanting.

The limited available data on ultraplankton uptake by coelobite sponges, derived from concentration differences between inhalant and exhalant waters and exhalant current velocities (Kötter et al. submitted), suggest intense mineralisation of the organic matter ingested. But attempts to measure the concomitant release of nutrients have been frustrated by the cryptic nature and small size of the specimen, as well as the methodological difficulty of determining low levels of nutrients in small volumes of water.

Indirect approaches, e.g. calculations based on the stoichiometric conversion of plankton carbon ingested to inorganic N and P released (Richter & Wunsch 1999, Richter et al. 2001, Kötter et al. submitted), are thwarted by the wide range of elemental ratios in near-reef waters (Atkinson & Smith 1983, D'Elia 1988, Smith & Kinsey 1988, Anderson & Sarmiento 1994) as well as the uncertainty how much of the plankton ingested is actually respired. Furthermore, the available measurements - carried out on coelobite specimen subjected to plankton-replete waters above the reef surface (Kötter et al. submitted) - may not reflect the actual metabolic rates in narrow crevices, where reprocessing of the water by the coelobite community causes strong spatial gradients (e.g. >70% Chl *a* depletions between near-reef and crevice waters, Richter & Wunsch 1999, Richter et al. 2001).

In the present study we used the plankton and nutrient changes in field enclosures to determine the filter feeding performance and mineralisation of coelobite sponges under simulated crevice conditions, where the temporal changes in the enclosed plankton and nutrients mimic the changes in the course of a parcel of water's Lagrangian drift through the porous framework. The aim was to compare both, coelobite versus non-coelobite (i.e. epi-reefal) sponges, as well as sponges with other active suspension feeders (here: ascidians).

Stoichiometric relationships between plankton carbon consumed and nutrients released were established and combined with measured and reported bulk community ultraplankton uptake rates to assess the importance of epi-reefal and coelobite suspension feeders in supplying new nutrients to the coral reef community.

Methods

Experimental design

Sponges for the *in situ* experiments were collected by SCUBA diving in March 2000 from the reef in front of the Marine Science Station Aqaba, Jordan. The following common species of coelobite and epi-reefal sponges were selected for experiments: *Callyspongia* sp. 2 and *Chondrilla* aff. *nucula* are epi-reefal sponges, whereas *Callyspongia* sp. 1, *Hemimycale arabica*, *Monanchora* sp., *Negombata magnifica*, *Chondrilla sacciformis*, *Chondrosia* aff. *reniformis* and *Tethya* aff. *seychellensis* are coelobite species (Table 1). The common ascidian *Didemnum* sp. occurred on the reef as well as in crevices. Ten individuals of each species were chiselled off the coral rock between 5-15 m depth and the attached substrate was cleaned of epibionts. Sponge fragments with a mean volume of 47 ml (minimum 0.5 ml, maximum 144 ml) were transferred into wire cages and left for 14 days at light levels similar to their original habitat, in a cave (cryptic) and on the reef (epi-reefal), respectively. This ensured protection from predation by fish and nudibranchs, recovery from transplantation trauma, and saturation of pore waters with ambient seawater concentrations. Potential uptake of ultraplankton by cleaned rubble was tested and proved to be insignificant after 90 minutes incubation.

Before each experiment the pumping activity of the sponges was inspected visually and only fully active animals were selected. Feeding experiments were carried out in two runs in the coral reserve in front of the Marine Science Station Aqaba. Sponges were transferred from their cages into 1.2 litre incubation chambers under water. The glass lid was sealed with a flat silicon ring. Six replicates of each species and three chambers filled with ambient seawater -serving as controls- were incubated under a coral overhang at 10 m depth. At the beginning of each experiment three ambient water samples were taken and immediately processed in the laboratory. After 90 min of incubation all experimental chambers were taken ashore to the laboratory of the Marine Science Station, stored in an icebox to minimize activity of sponges, plankton and bacteria, and processed within 1.5 h after collection.

Table 1. Sponges and ascidian* investigated during the study (Min - Max values). AFDM: ash-free dry mass

Species	**Ecotype**	**Morphotype**	**Color**	**Thickness** (cm)	**Sponge surface** (cm^2)	**AFDM** (g)	***n***
Callyspongia sp. 1	cryptic	crust	gray	0.8 - 1.0	11.2 - 44.1	0.62 - 1.81	12
Hemimycale arabica	cryptic	crust	blue	0.3 - 1.2	7.0 - 30.8	0.06 - 0.28	12
Monanchora sp.	cryptic	crust	light red	0.2 - 0.3	10.3 - 122.4	0.12 - 1.24	12
Negombata magnifica	cryptic	crust	red	0.5 - 1.0	6.6 - 15.0	0.29 - 0.73	6
Chondrilla sacciformis	cryptic	crust	light brown	0.2 - 0.3	10.8 - 48.5	0.86 - 4.14	12
Chondrosia aff. *reniformis*	cryptic	massive	dark brown	1.0 - 1.2	14.1 - 43.7	1.62 - 5.85	12
Tethya aff. *seychellensis*	cryptic	massive	red	2.8 - 3.5	12.6 - 38.5	0.37 - 1.28	12
Callyspongia sp. 2	epi-reefal	crust	brown	0.8 - 1.0	17.5 - 70.1	0.82 - 4.58	18
Chondrilla aff. *nucula*	epi-reefal	crust	dark purple	0.08 - 0.10	22.1 - 47.1	1.97 - 4.19	12
Didemnum sp.*	cryptic	crust	orange	0.09 - 0.12	23.9 - 47.2	0.31 - 0.69	6

Sample preservation and analysis

For separate counts of heterotrophic prokaryotes, prochlorophytes (*Prochlorococcus*), cyanobacteria (*Synechococcus*) and eukaryotes, 5 ml of water were preserved with paraformaldehyde solution (1% final concentration), kept dark and cool for less than 30 min and then frozen at -80°C.

Samples were analysed with a FACSort flow cytometer (Marie et al. 2000) at the Station Biologique de Roscoff, France. Data acquisition and cell counts were done with "CYTOWIN" software (Vaulot 1989).

Carbon content of picoplankton cells was estimated using the following cell to carbon conversion factors: 20 fg C $cell^{-1}$ for heterotrophic bacteria (Lee & Fuhrman 1987), 53 fg C $cell^{-1}$ for *Prochlorococcus* (Campbell et al. 1994), 250 fg C $cell^{-1}$ for *Synechococcus* (Kana & Glibert 1987) and 2096 fg C $cell^{-1}$ for eukaryotes calculated from the regression pg C= 0.433 × $(\text{body volume})^{0.863}$ (Verity et al. 1992) and an average cell volume of 6.22 μm^3 (Campbell et al. 1994).

For Chl *a* measurements, we filtered 3 replicates of 100 ml water samples onto 25 mm diameter GF/F filters (pore size 0.7 µm, Whatman). The pigments were extracted in 90% acetone for 24 h at 4°C in the dark and measured with a fluorometer (Turner designs Mod. 10-AU-005) using the acidification method (Parsons et al. 1984). We used a C-to Chl *a* conversion factor of 60 (Legendre et al. 1988).

Sample filtrates were used for spectrophotometric determination of ammonia, nitrite, nitrate and phosphate according to Parsons (Parsons et al. 1984). Oxygen was measured by Winkler titration (Grasshoff et al. 1976).

The surface area occupied by the experimental sponges was recorded under water with a digital video camera. The scaled images were analysed with the public domain software NIH-Image (http://rsb.info.nih.gov/nih-image/), whereas the thickness of each animal was measured *in situ* with calipers. Sponges were distinguished as two different "morphotypes": species of 1-10 mm thickness were categorized as "crusts" whereas those exceeding 1 cm thickness, growing as spheres (*Tehtya* aff. *seychellensis*) or in the shape of a potatoe (*Chondrosia* aff. *reniformis*) were categorized as "massive" growth forms. The sponges ranged from 6-122 cm^2 in size (Table 1).

Dry mass (*DM*) (24 h at 90°C) and ash free dry mass (*AFDM*) (5 h at 450°C) were determined for each specimen.

Retention efficiency (*RE*) in per cent was calculated for each animal and for each type of ultraplankton as:

$$RE = 100 \times (C_t - S_t) / C_t \qquad (1)$$

where $\boldsymbol{C_t}$ and $\boldsymbol{S_t}$ are the concentrations in the control and experimental chamber after the incubation time ***t***.

Clearance rates (*R*) were defined according to Riisgård (Riisgård 2001) as the volume of water cleared of suspended particles per unit of time of a standard weight suspension feeder (ml g AFDM^{-1} h^{-1}). They were calculated for all ultraplankton and nutrient groups according to Coughlan (Coughlan 1969):

$$R = \frac{V \times ln\ (S_t / C_t)}{m \times t} \qquad (2)$$

where ***V*** is the volume of the experimental chamber minus the volume of the animal (including substrate), ***m*** is the biomass of the specimen (g AFDM) and ***t*** is the incubation time.

The ultraplankton uptake rate *I* (µg C g AFDM^{-1} h^{-1}) was computed as:

$$I = R \times C_0 \times Cc \qquad (3)$$

where $\boldsymbol{C_0}$ is the particle concentration before the incubation (cells ml^{-1}) and ***Cc*** is the carbon conversion factor for ultraplankton cells.

As *Prochlorococcus* concentrations were below detection in some instances (Table 2), they were omitted for total ultraplankton calculations for conservancy.

We analysed data with a one-way ANOVA. Variables were log-transformed when variances were not homogenous and Scheffé tests were used for post-hoc comparisons. Unless otherwise denoted all values are median±MAD.

Results

In all experiments ultraplankton densities decreased significantly relative to controls after 90 min incubation (ANOVA, $p<0.05$) (Table 2).

Table 2. Initial concentrations (median ± MAD) in control chamber and % change in sponge chamber. Bac: heterotrophic bacteria, Pro: *Prochlorococcus*, Syn: *Synechococcus*, Euk: eukaryotes, Chl *a* : chlorophyll *a* . Initial samples were taken in triplicate for each species whereas number of samples for each sponge chamber varied between 6-18 (see Table 1). • below detection. * change not significantly different to initial concentration ($p>0.05$) according to one-way ANOVA.

Species	**Initial concentrations**					**% change**				
	Bac (10^6 cells ml^{-1})	**Pro** (10^4 cells ml^{-1})	**Syn** (10^4 cells ml^{-1})	**Euk** (10^3 cells ml^{-1})	**Chl *a*** ($\mu g\ L^{-1}$)	**Pro**	**Syn**	**Bac**	**Euk**	**Chl *a***
Callyspongia sp. 1	1.13 ± 0.27	1.05 ± 0.02	4.58 ± 3.35	6.52 ± 3.24	0.29 ± 0.03	•	98 ± 2	84 ± 3	78 ± 11	22 ± 23
Hemimycale arabica	0.97 ± 0.22	1.37 ± 0.06	5.67 ± 3.87	7.41 ± 2.77	0.21 ± 0.01	•	97 ± 1	75 ± 4	84 ± 3	31 ± 12
Monanchora sp.	0.89 ± 0.17	1.66 ± 0.03	2.32 ± 0.57	7.42 ± 1.73	0.21 ± 0.06	63 ± 3	77 ± 6	46 ± 8	58 ± 5	-3 ± 40*
Negombata magnifica	1.13 ± 0.03	3.23 ± 0.46	4.09 ± 0.19	5.37 ± 0.38	0.17 ± 0.01	76 ± 10	83 ± 6	57 ± 8	62 ± 9	22 ± 12
Chondrilla sacciformis	1.06 ± 0.57	0.92 ± 0.00	8.11 ± 5.94	7.11 ± 0.58	0.21 ± 0.01	•	79 ± 9	63 ± 12	63 ± 9	13 ± 10
Chondrosia aff. *reniformis*	1.12 ± 0.04	5.38 ± 0.46	3.29 ± 1.53	5.66 ± 0.29	0.15 ± 0.01	37 ± 14	57 ± 8	36 ± 12	37 ± 11	-14 ± 38*
Tethya aff. *seychellensis*	1.13 ± 0.49	0.92 ± 0.00	7.91 ± 6.14	7.10 ± 0.65	0.19 ± 0.13	11 ± 1	78 ± 22	64 ± 24	57 ± 22	-32 ± 25*
Callyspongia sp. 2	1.05 ± 0.21	1.07 ± 0.23	2.93 ± 0.79	10.13 ± 1.62	0.27 ± 0.03	•	99 ± 1	93 ± 4	91 ± 2	29 ± 13*
Chondrilla aff. *nucula*	1.17 ± 0.07	5.38 ± 0.46	3.20 ± 1.59	6.65 ± 1.23	0.19 ± 0.04	55 ± 10	62 ± 19	41 ± 18	44 ± 15	41 ± 57*
Average sponge	1.09 ± 0.26	1.62 ± 0.70	2.93 ± 1.29	7.52 ± 1.97	0.21 ± 0.05	60 ± 16	84 ± 15	66 ± 21	63 ± 22	14 ± 24
Didemnum sp. *	1.13 ± 0.03	3.23 ± 0.46	4.09 ± 0.19	5.37 ± 0.38	0.17 ± 0.01	44 ± 4	59 ± 7	5 ± 5*	42 ± 3	33 ± 11

Depletions were highest for *Synechococcus* in all species investigated (84±15%). All sponges had similar retention efficiencies for the other ultraplankton groups, depleting *Prochlorococcus,* heterotrophic bacteria and eukaryotes by 60-66%.

The ascidian *Didemnum* sp. showed a lower overall performance, particularly on the smallest plankton fraction, which was not depleted significantly.

Chl *a* depletions amounted to 33±11% in the ascidian *Didemnum* sp. and only 14±24% in sponges. In all experiments Chl *a* concentrations were homogenous at the beginning of the experiments (0.21±0.05) but highly variable after incubation. Some experiments showed even net Chl *a* enrichments (Table 2).

Total ultraplankton uptake was significantly different between morphotypes (F=10.52, df=1, p=0.001) and ecotypes (F=5.49, df=1, p=0.02): sponges growing as crusts consumed nearly five times more ultraplankton (57±46 µg C g AFDM^{-1} h^{-1}) than massive animals (12.0±8.7 µg C g AFDM^{-1} h^{-1}), with heterotrophic bacteria, *Synechococcus* and eukaryotes taking equal shares of the diet in both groups (Fig. 1a).

Coelobite sponges had higher ultraplankton uptake rates (54.2±47.4 µg C g AFDM^{-1} h^{-1}) than epi-reefal sponges (45.1±36.5 µg C g AFDM^{-1} h^{-1}) (Fig. 1b). This pattern prevailed in all ultraplankton fractions. In comparison, the ascidian *Didemnum* sp. had a rather low uptake (29.6±8.9 µg C g AFDM^{-1} h^{-1}).

Clearance rates were highly variable in coelobite (124±51 to 9387±4779 ml g AFDM^{-1} h^{-1}) and epi-reefal sponges (129±56 to 1056±391 ml g AFDM^{-1} h^{-1}) and amounted to 907±333 ml g AFDM^{-1} h^{-1} in the ascidian.

Linear regression showed no correlation between initial concentrations of ultraplankton and uptake rates (n= 108, p> 0.5).

Nutrient levels increased in all but one experiment relative to controls. Both, TIN (total inorganic nitrogen) and phosphate were significantly different between ecotypes (F=18.79, df=1, p<0.0001 and F=8.19, df=1, p<0.01, respectively) but not between morphotypes. Coelobite sponges released four times more TIN and two times more phosphate than epi-reefal sponges (0.51±0.41 µmol g AFDM^{-1} h^{-1} and 0.07±0.05 µmol g AFDM^{-1} h^{-1}, respectively) (Table 3). In spite of a higher TIN release by the ascidian, it released less phosphate than the sponges (0.72±0.16 µmol g AFDM^{-1} h^{-1} and 0.06±0.03 µmol g AFDM^{-1} h^{-1}, respectively). Composition of TIN did not vary significantly between ecotypes, where ammonia (72-84%) was followed by nitrate (17-20%) and nitrite (less than 4%).

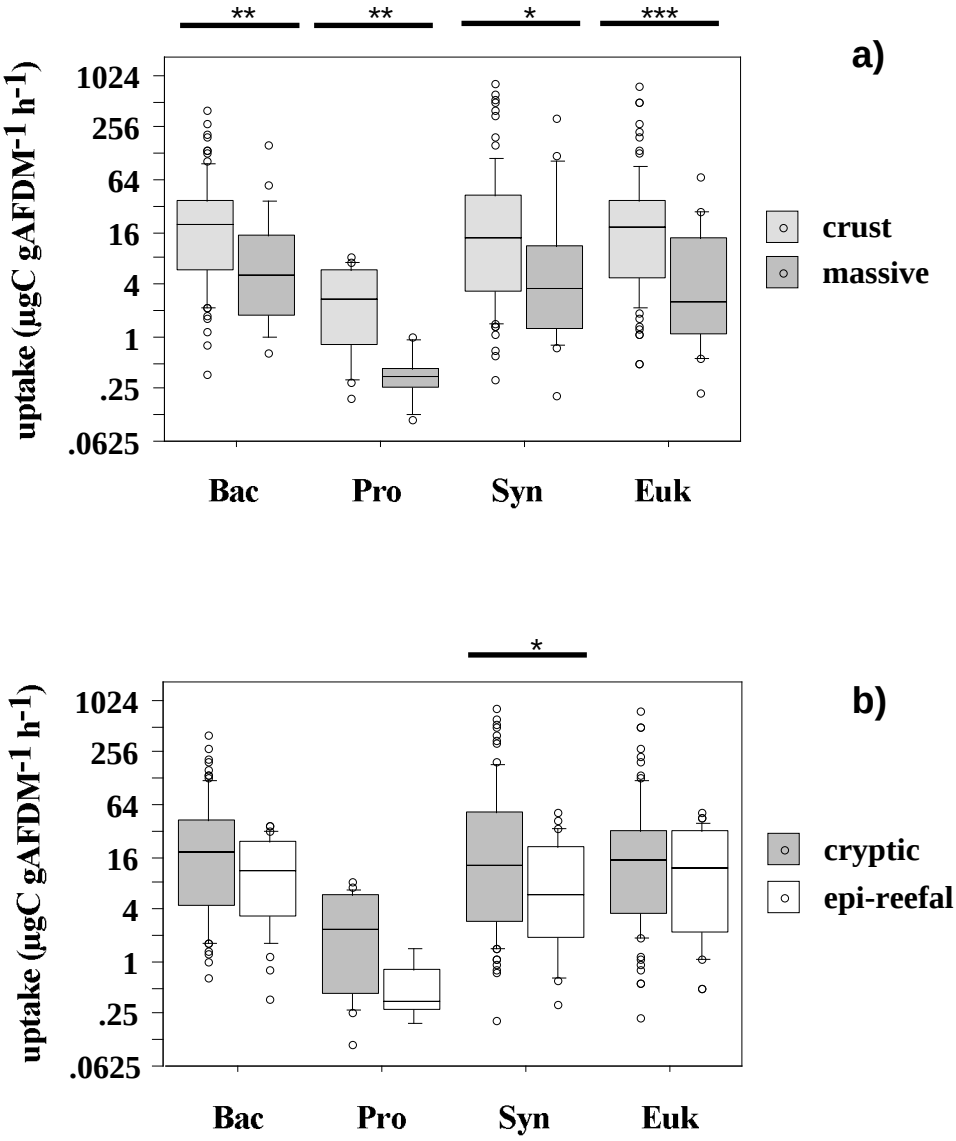

Fig. 1 a+b Median and ranges of various fractions of ultraplankton uptake depending on sponge morphotype **(a)** and ecotype **(b)** (see text for definition). Boxes encompass 50% of the data between the 25th and 75th percentile, center lines display the medians. The upper and lower horizontal lines delimit the 10th and 90th percentiles, outliers are shown as open circles. **Bac:** heterotrophic bacteria, **Pro:** *Prochlorococcus***, Syn:** *Synechococcus***, Euk:** eukaryotes. Bars above boxes denote significant differences according to one-way ANOVA, * $p<0.01$, ** $p<0.001$, *** $p<0.0001$.

Table 3. Stoichiometry of carbon, nitrogen and phosphorus. Values denote median ± MAD (µmol g $AFDM^{-1}$ h^{-1}) of sponges and ascidian.
C: ultraplankton carbon, TIN: total inorganic nitrogen, calc.: calculated according to the Redfield ratio (C:N:P= 106:16:1), (positive values denote enrichment, negative values depletion).

Parameter	**Sponges**		***Didemnum* sp.**
	Epi-reefal	**Coelobite**	
Δ C	-3.755 ± 3.083	-4.510 ± 3.940	-2.464 ± 0.741
Δ TIN	0.142 ± 0.058	0.505 ± 0.410	0.716 ± 0.159
Δ PO_4^{3-}	0.026 ± 0.015	0.065 ± 0.047	0.064 ± 0.033
C: N ratio	26.4	8.9	3.4
C: N: P ratio	144: 6: 1	69: 8: 1	39: 11: 1
calc. Δ TIN	0.567	0.681	0.372
calc. Δ PO_4^{3-}	0.035	0.043	0.023

Discussion

This study provides the first quantitative data on nutrient cycling by coelobite sponges, and a comparative evaluation of ultraplankton uptake and mineralisation in coelobite and epi-reefal filter feeders. Nutrient enrichments with concomitant depletions of bacteria, prokaryotic and eukaryotic algae show effective mineralisation of ultraplankton in all groups. Coelobite sponges featured particularly high bacterial uptake rates (Fig. 1b) and low ΔC:ΔN and ΔC:ΔP ratios (Table 3), indicating a high proportion of bacteria ((C:N= 4.2, Nagata 1986) and C:P= 7-76, (Vadstein et al. 1988)) in the diet. The ΔC:ΔN ratios of epi-reefal sponges, by contrast, are near the Redfield ratio (Table 3), suggesting that a higher fraction of larger eukaryotic plankton is consumed. These findings support earlier predictions (Richter 1998, Richter & Wunsch 1999, Richter et al. 2001) that microphagy in coral reef planktivores increases with growing distance from the source: whereas large and mid-sized particles are intercepted by zooplanktivorous fish hovering reef upstream (Hamner et al. 1988) and tentaculate and mucus-net feeding invertebrates at the reef-water interface (Porter 1974, Sebens et al. 1996, Kappner et al. 2000), the smallest particles are captured by filter feeders dwelling at or within the reef framework.

As a result, both plankton load and size decreases from the exposed reef to the framework crevices. Coelobite sponges, moderately efficient under plankton-replete experimental conditions (Kötter et al. submitted), seem particularly efficient for small-celled bacterioplankton in plankton-depleted simulated crevice conditions (this study). High feeding efficiencies of encrusting morphs (Fig. 1a) may help explain why almost all coelobite filter feeders are sheet-like forms (Richter et al. 2001). While the succession from sheet-like delicate to massive and erect forms in benthic suspension feeding communities has been attributed to hydrodynamic gradients governing the supply of exogenous food and, hence, exploitational opportunities (cf. (Gili & Coma 1998)), our results suggest additional, intrinsic, advantages of being flat: sheet-like growth offers higher retention efficiency, probably due to the higher surface:volume ratio compared to massive growth. It also reduces the risk of physical damage by sheltering fish (unpubl. observ.)

Where predation is intense, such as the exposed reef surface, massive growth forms prevail (Wulff 1988, Pawlik 1998). Their lower retention efficiencies (Fig. 1a) may be overcome by both, a generally higher advective supply of food, and a high slenderness ratio (body height: width ratio, Abelson et al. 1993) providing access to food above the food-depleted boundary layer.

The high levels of NH_4^+ in the incubations (>70% of N) corroborate earlier assumptions that a significant part of the observed NH_4^+ enrichments in coral reef crevices (Richter et al. 2001, Scheffers et al. 2002, van Duyl et al. 2002) is due to coelobite sponges. Differences in NH_4^+ concentrations between incubations and framework crevices (42% of N, Richter et al. 2001) may be due to either bacterial nitrification (e.g. (Kirchmann 1994)) and/or preferential assimilation of NH_4^+ by phototrophs (e.g. sciaphilic coralline algae and corals) near the crevice entrances (Sorokin 1995).

The processes of nitrification and NH_4^+-assimilation have been internalised by some symbiont-bearing epi-reefal sponges (Wilkinson & Fay 1979, Corredor et al. 1988, Diaz & Ward 1997), resulting in near-complete conversion of excretory NH_4^+ to NO_3^-. Although the sponges investigated in this study do harbour associated micro-organisms (Kötter et al., unpubl. data), the absence of any substantial NO_3^- release in our experiments (<20% of N, no significant differences between coelobite and epi-reefal sponges) suggests that microbial-sponge associations are no major nitrification pathway in framework crevices.

Microbial associations with colonial didemnid ascidians (Larkum et al. 1987) may offer an explanation for the particularly low ΔC:ΔN and ΔC:ΔP ratios in *Didemnum* (Table 3). The very low values may be due to microbially-enhanced mineralisation of DON and DOP, which leads to excess ΔN and ΔP relative to ultraplankton-derived excretory N and P.

The lack of covariance in our results between Chl *a* and phototroph ultraplankton concentrations are startling (Table 2). The mismatch may be due to differential growth and grazing mortality in ultraplankton and larger (>10 µm) algal populations, respectively: the former are detected by both, flow cytometer and Chl *a* method, whereas the latter is detected by the Chl *a* method only, leading to the apparent discrepancy. In the Chl *a* measurements, low grazing mortality and nutrient-enhanced growth of the larger algal size fractions may have masked or counterbalanced depletions in the ultraplankton, resulting finally in only moderate net depletions (or even enrichments in some cases, Table 2). Analytical errors can be ruled out: Chl *a* filters were processed in random order and controls were virtually constant (0.21±0.05 µg l^{-1}, Table 2).

A second explanation may be that the sponges are losing larger (>10 µm) algal symbionts (zooxanthellae, or clusters of cyanobacteria). This would support earlier reports of coral reef sponges' dual role as net sinks of prokaryotic cell types, and as net sources of eukaryotic algae (Pile 1997). It is not clear to date to what extent coelobites harbour algal symbionts, but major sponge-algae associations seem unlikely in dark habitats. Moreover, it is difficult to envision, from an energetic point of view, how expulsion of such symbionts may have evolved under chronic food-scarcity of crevices.

The clearance rates of coelobite sponges examined in this study are similar to those of coelobite sponges living in the Caribbean (9825±6592 ml g $AFDM^{-1}$ h^{-1} (mean±SD), Kötter & Pernthaler in press). Those for epi-reefal sponges are within the range of clearance rates reported for other tropical sponges like *Verongula* sp. and *Verongia gigantea* (3054 and 264-4470 ml g $AFDM^{-1}$ h^{-1}, respectively, Reiswig 1974) as well as temperate sponges (Riisgård et al. 1993, Ribes et al. 1999).

Likewise, ultraplankton uptake rates of epi-reefal and coelobite sponges are similar to those reported for other tropical and temperate sponges (Table 4). These incubation figures are lower than those reported from direct measurements. Kötter (Kötter et al. submitted), comparing plankton concentrations from free-stream and exhalant oscular waters (Table 4) found two times higher uptake values for coelobites. The discrepancy was even higher for

Table 4. Biomass-specific ultraplankton uptake and clearance rates for sponges and other filter-feeders.

Values are median±MAD unless otherwise denoted by symbols. *: arithmetic mean, †: range; #: calculated

Species	Ecotype	Study site	Ultraplankton uptake [µg C g (AFDM)$^{-1}$ h^{-1}]	Reference
Sponges (marine)				
Callyspongia sp. 1	cryptic	Red Sea	60 ± 27	this study
Hemimycale arabica	cryptic	Red Sea	707 ± 197	this study
Monanchora sp.	cryptic	Red Sea	64 ± 41	this study
Negombata magnifica	cryptic	Red Sea	106 ± 15	this study
Chondrilla sacciformis	cryptic	Red Sea	11 ± 4	this study
Chondrosia aff. *reniformis*	cryptic	Red Sea	5 ± 2	this study
Tethya aff. *seychellensis*	cryptic	Red Sea	46 ± 29	this study
several species	cryptic	Red Sea	127 ± 109	Kötter et al. submitted
several species	cryptic	Caribbean	70 ± 60 #	Kötter & Pernthaler in press
Callyspongia sp. 2	epi-reefal	Red Sea	50 ± 15	this study
Chondrilla aff. *nucula*	epi-reefal	Red Sea	6 ± 3	this study
several species	epi-reefal	Red Sea	569 ± 351	Kötter et al. submitted
Verongia fistularis	epi-reefal	West Atlantic	64 ± 9 *#	Reiswig 1981
Dysidea avara	epi-reefal	Mediterranean	10 - 183 †	Ribes et al. 1999
Ascidians				
Didemnum sp.	cryptic	Red Sea	30 ± 9	this study
Halocynthia papillosa		Mediterranean	1305 ± 496*	Ribes et al. 1998

epi-reefal sponges (up to one order of magnitude), suggesting that epi-reefal sponges perform much better in plankton-rich conditions where an increase in pumping rate allows an increased food uptake. Where the supply of food is low, such as in crevices, an increase in retention efficiency is the only way to gain more food. Higher pumping would result in refiltration only.

We combined the results of this study with the biomass of coelobite (21.1 g sponge C m^{-2} (Richter et al. 2001) and epi-reefal (0.6 g sponge C m^{-2} (Kötter et al. submitted) suspension feeders in Red Sea coral reefs, with ultraplankton uptake rates of 0.6±0.36 g C m^{-2} d^{-1} (Kötter et al. submitted) as upper margin: a total 5.8 mmol N and 0.7 mmol P are harnessed per projected m^2 of coral reef.

These findings indicate potentially important reciprocal effects between filter feeding benthos and plankton communities: selective feeding by the filter feeding coral reef biota may shift the biomass-size spectrum from ultraplankton-dominated in the incident oceanic waters (Ducklow 1990) to nano- and microplankton-dominated in the waters aloft (this study, cf. also (Pile 1997)). The fate of the plankton- and nutrient-altered waters flowing off the reef merits further attention.

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Communities of coral reef cavities in Jordan, Gulf of Aqaba (Red Sea)

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Abstract Cavities are a ubiquitous feature of coral reefs offering a large substrate to benthic organisms (coelobites). Due to their small size very little is known about the communities lining their walls. Using the video-endoscopic CaveCam we investigated the community composition of coral reef cavities in a Red Sea fringing reef. Cavities measuring 0.2-0.6 m in diameter and 1.25-1.75 m in length were studied at depth between 2-20 m. From 1486 close-up images a total of 274 macrobenthic taxa was distinguished covering 59% of the total available substrate. Algal cover decreased from 60% at the cavity entrance to below 20% at 0.75 m distance from the entrance. Conversely faunal cover increased from less than 20% near the entrance to up to 40% within the cavities and consisted mainly of sponges (15.9%), polychaetes (5.6%), scleractinian corals (2.2%) and ascidians (1.8%). Light and water flow were the main factors governing the zonation within cavities, whereas water depth and water flow determined the community differences between cavities.

Keywords Caves, Cavities, Coral reef, Image analysis, Underwater video, Benthic communities, Coelobites

Introduction

Coral reefs are commonly perceived as massive limestone formations. However, their framework is rather hollow, riddled with holes and crevices providing extensive substrate for a wide range of benthic organisms (Jackson et al. 1971) as well as shelter for many vagile animals (Kobluk 1981). Cryptic habitats originate from complex interactions between coral growth and bioerosion, as well as from collapse and solution of the framework (Bonem 1977, Logan et al. 1984). Two extreme types have been investigated extensively: large caves, that are easily accessible by conventional SCUBA diving (Vasseur 1974 and 1981, Logan 1981, Macintyre et al. 1982, Logan et al. 1984), and the undersides of easily collectible coral fragments, known as coral rubble (Choi & Ginsburg 1983, Choi 1984, Meesters et al. 1991, Gischler & Ginsburg 1996, Gischler 1997).
However the ubiquitous crevices, cracks and small caves (0.05-1 m in diameter) have so far been neglected. The recent development of the CaveCam (Wunsch & Richter 1998) now provides an appropriate tool for the exploration and monitoring of these hidden habitats in a non-destructive way.
As part of a larger study of coelobite communities in the Red Sea, the aim of this work was:

1) To quantitatively describe the coelobite communities in 'typical' 0.2-0.6 m diameter coral reef cavities in the northern Gulf of Aqaba using the CaveCam
2) To identify factors controlling the composition of coelobite communities and to assess their importance

Materials and methods

Site description

The study sites were located in a marine reserve in front of the Marine Science Station (MSS) at the northeastern coast of the Gulf of Aqaba, Jordan (29°27'N, 34°58'E). The Gulf is one of the two northern extensions of the Red Sea. It is characterized by fringing coral reefs existing at their upper northern latitudinal limit, subjected to large seasonal variations of water temperature (20-27 °C), relatively calm water and weak currents (5.2 cm s^{-1} on average, rarely exceeding 20 cm s^{-1}, Manasreh 1998).

Sampling design and survey methods

The sampling design accounted for differences between depths (shallow-medium-deep with water depths ranging between 2-3 m, 11-13 m and 19-20 m, respectively), distance from the cavity entrance (in 25 cm increments or 'slices' between 0-175 cm) and substrate orientation (ceiling, left and right wall, bottom). Parameters measured included: abundance in percent cover of coelobite taxa, light intensity, water exchange, as well as various measures of cave morphology. Cavities matching the criteria of length (1.25-1.75m) and opening diameter (<1 m) were selected haphazardly by diving along the predefined depth.
The sessile communities lining the inner surface of the cavities were sampled with the CaveCam, a 25 mm diameter high-resolution endoscope-like camera (Wunsch & Richter 1998). The camera head was equipped with a 7.5 mm wide-angle lens and a 45° mirror device to allow perpendicular close-ups of cave walls at a frame size of 6 x 4.5 cm. The head was mounted on the flexible end of a 130 cm long 1 × 1 cm aluminium profile.
Sampling routine: Along the cave axes, for every 25 cm 'slice,' a set of 20 frames was recorded, 5 frames of each 'orientation': roof, bottom, left and right side. Thus the average 1.5 m cavity yielded a total of 140 frames, representing an area of 3780 cm^2. Coelobite cover is given in relative units. Cavity volume, surface area and morphological features were assessed by means of the LightSheet, a CaveCam based underwater surveying system (Wunsch, submitted). It produces successive cross-

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sections of the cavities along their axis from which the 3-D outlines of the caves can be reconstructed. From these data we calculated cave volume and wall area.

Image analysis

Image analysis was performed on an Apple Macintosh with a frame grabber card and a digitizing tablet. We customized the public domain software NIH-Image (developed by W. Rasband at the U.S. National Institutes of Health, available at http://rsb.info.nih.gov/nih-image/) to our purpose. Individual organisms, substrate, unidentifiable crusts and void areas (i.e. black background in a part of the image) were outlined manually with the digitizing pen and recorded as percent. Organisms were specified, if possible, to species or nearest taxonomic level.

Water exchange rates

Water motion was measured with the 'clod card' technique (Jokiel & Morrissey 1993). Dissolution rates were calibrated with a SD-6000 current meter (by Sensordata AS, Norway) in the field: sets of 6 replicate blocks were moored next to the current meter for 48 h periods under different current regimes. A reference set was placed in a closed 50 l barrel in the reef to simulate zero current conditions. Current meter readings were averaged over the respective 48 h for the calibration curve. The regression yielded a good fit:

Current speed (cm s^{-1})= -2.22 + 5.45 * weight loss (% h^{-1}); R^2 =0.93

Gradual differences of water exchange rates along the cave axis were measured with 2 m long aluminium profiles equipped with 4 pairs of plaster blocks, one pair each for the end, the middle, the cave entrance and the open water (approximately 50 cm from the cavity entrance). One block per pair was hung on wire hooks 10 cm to both sides of the profile. These were then concurrently placed along the cave axis for 48 h. This procedure was repeated 3 times. Results were averaged over time.

Light measurements

A miniaturized light-meter with a high sensitivity (flat) cosine collector (ø 10 mm) on a 4 m long cable was designed to measure the light intensity with increasing distance from the cavity entrance. Duplicate readings were taken from each 'orientation' resulting in 4 x 2 readings per "slice". The duplicate values were averaged and displayed as percent of the surface radiation.

Statistical analysis

Community analyses were performed on a subset of data excluding the rare species (Clarke & Warwick 1994). A combination of the overall contribution to the cryptofauna cover (>125 area units) and to the total numerical abundance of a taxon (n>100) qualified 37 taxa for this analysis. Because of unequal length of the cavities investigated, only the first 6 slices were considered. We applied a variety of analytical techniques to examine the distribution and structure of distinct coelobite assemblages as well as their relation to environmental parameters (depth, water motion, cavity size, form etc.). These are part of the PRIMER 4.0 software package for multivariate statistics (developed by K. R. Clarke and R. M. Warwick at the Plymouth Marine Laboratory). The relationships between community patterns and the environmental parameters were analyzed with the multivariate BIO-ENV procedure (Clarke 1993). Non-parametric multidimensional scaling (MDS) with the Bray-Curtis measure for similarities and 4^{th}-root transformation was applied to display the stations in a two-dimensional plot reflecting their biological similarities (Kruskal & Wish 1978).

Reference sampling

Parallel to the video surveys 120 coelobites were photographed *in situ*, removed and fixed according to respective protocols and sent to the following experts for identification: R. van Soest, University of Amsterdam, Netherlands (sponges); M. Grasshoff, Research Institute Senckenberg, Germany (gorgonians); K. Fabricius, Australian Institute of Marine Science, Australia (soft corals); D. Fenner, J. E. N. Veron, Australian Institute of Marine Science, Australia (hermatypic corals); H. Zibrowius, Marseille, France (ahermatypic corals); J. Scholz, Senckenberg Research Institute, Germany (bryozoans); L. Hottinger, Natural History Museum, Basel, Switzerland (foraminifers); P. Kott, Queensland Museum Brisbane, Australia (ascidians); Derek Keats, University of the Western Cape, South Africa (encrusting algae).

Results

Table 1 summarizes the main characteristics of the 12 cavities. They were grouped into three categories by their general structure: (1) dead ending 'sack-type' cavities, (2) tunnels with subsidiary arms connecting to neighbouring cavities and (3) tunnels that have a rather open structure as found regularly close to the reef crest.

Table 1 Characteristics of cavities.

Code	Depth (m)	Cavity type	Total length (cm)	Cavity volume (l)	Inner surface (m^2)	Water motion (cms^{-1})	SE (cm s^{-1})
Aq 1	2	open tunnel	175	456	4.2	4.3	0.2
Aq 2	2	open tunnel	150	564	3.8	3.8	0.3
Aq 3	2	open tunnel	150	303	3.7	2.8	0.1
Aq 4	2	open tunnel	150	483	4.7	3.6	0.0
Aq 5	12	tunnel/arms	150	298	3.7	1.7	0.1
Aq 6	13	open tunnel	150	334	3.2	2.1	0.0
Aq 7	13	open tunnel	150	428	4.0	2.0	0.1
Aq 8	13	sack	150	542	4.5	1.4	0.1
Aq 9	19	sack	150	361	3.5	2.1	0.4
Aq 10	19	sack	125	288	3.4	2.2	0.5
Aq 11	20	tunnel/arms	150	224	3.0	2.5	0.2
Aq 12	19	sack	150	249	2.9	1.8	0.2

With the exception of cave Aq3, flushing was highest in the shallow caves with wave driven currents of up to 4.3 cm s^{-1}. The swell was generally weak but waves hampered the work on two days in shallow waters. The caves tend to funnel impinging waves with subsequent acceleration of the water. Weak flushing was typical for 'sack-type' caves. We found lowest values (1.4 cm s^{-1}) in Aq8, which is situated in sheltered habitats near the bottom of a canyon.

Table 2 Relative cover (%) of major taxa and substrates (without cave bottom).

		shallow 2-3 m				medium 11-13 m				deep 19-20 m					
Higher taxa and substrates	**No. of lower taxa**	**Aq1**	**Aq2**	**Aq3**	**Aq4**	**Aq5**	**Aq6**	**Aq7**	**Aq8**	**Aq9**	**Aq10**	**Aq11**	**Aq12**	**Taxon average**	**SD**
Algae	**28**	32.88	26.07	16.82	32.04	54.23	33.03	48.04	38.67	20.73	29.56	23.21	30.91	32.18	10.76
Foraminifera	**4**	0.58	0.12	0.20	0.06	0.20	0.12	0.12	0.02	0.04	0.01	0.01	0.02	0.12	0.16
Porifera	**133**	17.26	25.38	16.72	15.30	8.55	26.67	14.96	5.66	21.40	15.34	17.89	5.68	15.90	6.79
Hydrozoa	**4**	0.02	0.01	0.05	0.02	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.02
Octocorallia	**8**	0.27	0.09	0.16	0.27	1.64	1.36	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.57
Scleractinia	**20**	6.78	2.25	1.91	3.99	1.40	2.04	1.82	0.01	2.02	0.84	2.07	1.41	2.21	1.71
Polychaeta	**14**	0.39	0.11	0.08	0.11	0.14	0.17	0.17	0.71	12.28	9.01	30.83	13.05	5.59	9.43
Mollusca	**4**	0.00	0.00	0.00	0.03	0.00	0.01	0.02	0.06	0.00	0.01	0.05	0.00	0.02	0.02
Bryozoa	**13**	0.77	0.83	0.05	0.06	0.63	0.07	0.12	0.20	0.29	0.21	0.04	0.03	0.28	0.30
Ascidia	**23**	1.93	3.59	3.96	0.57	1.16	2.16	2.19	2.81	1.19	0.51	1.68	0.31	1.84	1.18
Other Taxa	**23**	0.93	1.62	2.19	0.16	1.09	1.20	0.27	0.12	0.05	0.19	0.02	0.03	0.66	0.73
Miscellaneous		9.69	22.81	14.76	15.97	4.54	2.41	2.11	1.45	5.65	3.98	7.29	2.58	7.77	6.76
Microfacies		27.99	16.24	40.70	30.34	18.48	19.69	15.89	25.01	31.34	31.58	15.38	39.12	25.98	8.94
Unidentified		0.52	0.28	0.10	0.00	2.96	7.87	12.62	24.28	4.61	8.66	1.53	6.87	5.86	7.09
Sediment		0.00	0.61	2.30	1.09	4.97	3.19	1.67	1.00	0.40	0.11	0.00	0.00	1.28	1.54
Total	**274**	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	
Total taxa per cave		**97**	**105**	**95**	**76**	**56**	**81**	**66**	**52**	**67**	**73**	**53**	**50**		

Inventory and diversity of coelobites

Diverse cryptic communities were encountered at all three depths. All together, 274 taxa were distinguished from a total of 1486 video close-up images representing an area of more than 4 m^2 of cavity habitat. An overview of the major groups with their relative cover and species diversity per cave is summarized in Table 2. The largest part of the sampled area (59%) could be assigned to macrobenthic taxa and 7.8% to unidentifiable macrobenthos. The remaining substrate was classified either as sediment, microfacies (a rocky substrate with reddish to brownish coloration) or unidentifiable hard substrate. Sponges were by far the most diverse group (133 taxa) comprising up to 45% of the live cover (27% in average). Algae were represented by 28 taxa covering the largest area (54.5% of the live cover). Polychaetes were locally abundant and reached an overall average of 9.5% cover, but mainly in the deeper cavities. This was mainly due to monospecific crusts that occurred in several caves. It was not clear if all individual tubes of these crusts were still inhabited by worms or if the empty ones had built up over time. Ascidians, scleractinians and octocorals were patchily distributed with a low overall coverage of 0.3–2.2%. Within the ascidians the colonial Didemnidae represented almost one third of the 23 taxa but comprised over 73% of the area colonized by ascidians. The scleractinian corals are divided into two major groups: the so-called reef-building or hermatypic corals, and the ahermatypic corals with representatives of the families Dendrophyllidae and Caryophyllidae. The latter may occur locally in large numbers on the cavity ceilings. The taxa identified to either genus or species level are listed in Table 3. Multivariate statistical analyses were carried out to identify possible environmental factors and to assess their importance with regard to the observed changes in coelobite communities.

The MDS-ordination (Fig.1) clearly illustrates differences between coelobite communities in shallow (2 m) and deeper water (12-20 m) (stress factor of only 0.09). The communities in deeper water seem to be rather similar, as they congregate in one area.

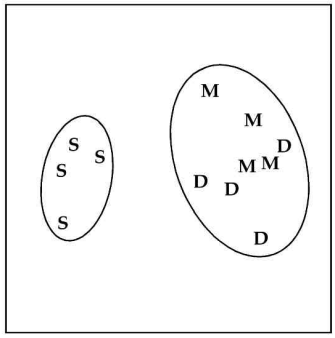

Fig. 1 Non-parametric MDS ordination plot of the 12 cavities, labelled according to depth: S = shallow 2-3 m, M = medium 11-13 m, d = deep 19-20 m. Based on 4^{th}-root transformed abundances (= cover) of the 37 most abundant taxa and Bray-Curtis similarities (stress = 0.09).

Separate BIO-ENV analyses were carried out to test for (1) vertical and (2) horizontal differences in coelobite communities between and within cavities. The former was a depth comparison of cavities averaged horizontally across slices, the latter a slice by slice analysis of a composite cavity averaged across depths and sites. BIO-ENV analyzes the relation between the coelobite distribution and combination of environmental variables, at a time, yielding the 'best matches' of biotic and abiotic

Table 3 List of all taxa identified to genus or species level.

Algae	*Chelonaplysilla erecta*	*Haliclona sp. 3*	*Terpios cruciatus*	**Other Hexacorallia**
Peyssonellia sp. leafy	*Chondrilla sacciformis*	*Haliclona sp. 4*	*Tethya seychellensis*	*Anthipates sp.*
Foraminifera	*Chondrosia aff. reniformis*	*Haliclona sp. 5*	*Tethya sp. 1*	**Polychaetes**
Gypsina plana	*Clathria sp. 1 (whitish)*	*Haliclona sp. 6*	*Timea sp.*	*Filograna sp.*
Halyphysema sp.	*Clathria sp. 3 (yellow)*	*Haliclona sp. 7*	**Sea anemones**	*Sabella sp.*
Homotrema rubrum	*Clathria sp. 5*	*Haliclona strongyles*	*Palythoa sp.*	**Molluscs**
Sponges	*Clathria sp. 6 (beige)*	*Hymedesmia sp. 1*	*Triactis producta*	*Gastrochaena sp.*
Acanthella cavernosa	*Clathria sp. 8 (white)*	*Leucetta chagosensis*	**Octocorals**	*Lithophaga sp.*
Aiolochroia praetensa	*Clathrina sp. 1*	*Leucetta philipensis*	*Acabaria erythraea*	**Bryzoans**
Antho sp.	*Clathrina sp. 2 (tiny)*	*Leuconia aff. armata*	*Acabaria sinaica*	*Buskea sp.*
Aphroceras sp.	*Clathrina sp. 4*	*Monanchora sp. 1*	*Dendronephthya sp.*	*Celleporaria fusca*
Aplysilla sp. 1	*Cliona sp. 1 (red)*	*Monanchora sp. 2*	*Scleronephthya sp.*	*Celleporaria sp. 2*
Aplysilla sp. 2	*Cliona sp. 2 (green)*	*Mymekioderma granulata*	*Siphonogorgia mirabilis*	*Iodictium sp.*
Arenosclera sp. 1	*Cliona sp. 3 (vine red)*	*Petrosia sp. 1*	**Scleractinians**	**Ascidians**
Arenosclera sp. 2	*Cliona sp. 4*	*Phorbas sp.*	*Dendrophyllia sp. 1*	*Aplidium crateriferum*
Artemisina sp. 1	*Crella cyathophora*	*Placospongia sp. 1*	*Dendrophyllia sp. 2*	*Didemnum molle*
Ascandra sp.	*Dendroxea sp.*	*Plakortis sp.*	*Dendrophyllia sp. 3*	*Didemnum sp. 1 white*
Batzella sp. 1 (red)	*Euryon sp.*	*Pleraplysilla sp.*	*Echinophyllia aspera*	*Didemnum sp. 2 red*
Batzella sp. 2	*Euryspongia sp. (beige)*	*Pseudaxinella sp.*	*Pavona aff. explanulata*	*Didemnum sp. 3 white*
Batzella sp. 3 (green)	*Grantilla hastiferata*	*Scopalina sp. 1*	*Psammocora (explanulata)*	*Didemnum sp. 4 white*
Batzella sp. 4	*Grantilla scylloides*	*Scopalina sp. 2*	*Psammocora sp. 1*	*Didemnum sp. 5 pink*
Callyspongia sp. 1	*Grantilla sp.*	*Stylissa massa*	*Seriatopora hystrix*	*Didemnum sp. 6*
Callyspongia sp. 2	*Haliclona sp. 1*	*Sycon sp.*		*Eusynstyela latericius*

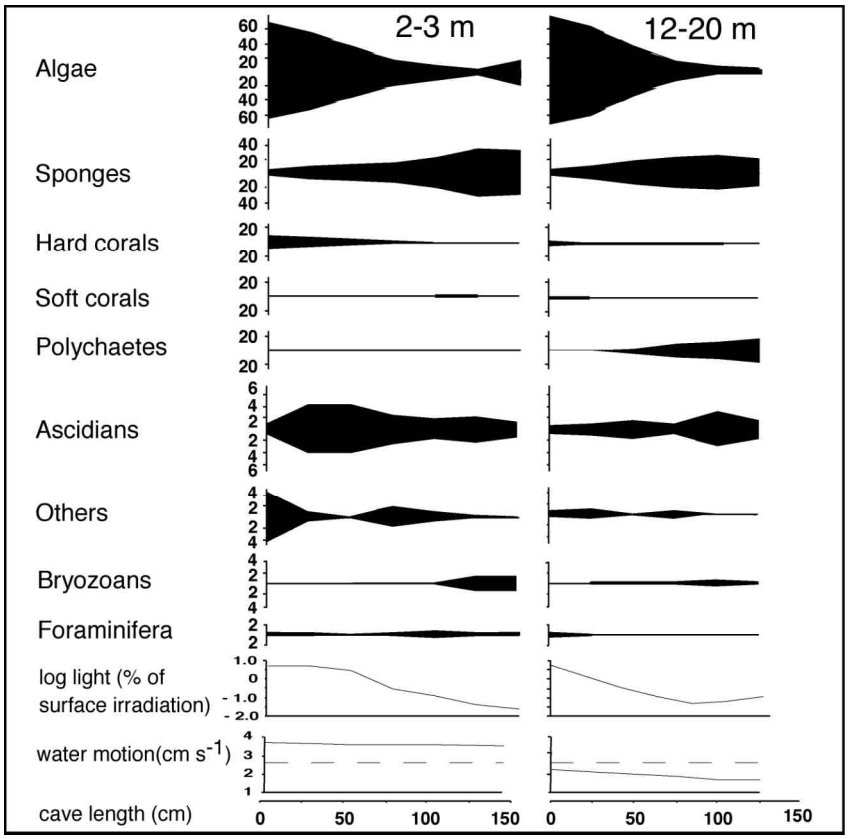

Fig. 2 Distribution of coelobite communities in shallow and deeper cavities, light values and water motion (dotted line resembles open water value). Note the ten-fold magnification of the scale of rarer taxa, starting with ascidians.

similarity matrices for each combination as measured by standard Spearman harmonic rank correlation ρ_H.
(1) Depth was found to be the most important factor influencing the composition of coelobites (ρ_H=0.66). However water motion (ρ_H =0.47) and volume flushing, i.e. the product of water exchange rate and slice cross-sectional area (ρ_H =0.45), were also important.
(2) The factors influencing the zonation within the cavities were investigated in the same way. For the community zonation depth remained the single most important determinant (ρ_H=0.29) but the factor distance from cavity entrance was almost as important (ρ_H=027). Combined with light these two showed the highest correlation (ρ_H=0.43).

Distribution of higher taxa

The spatial distribution of the higher coelobite taxa, illumination and water exchange is displayed in Fig. 2. Data were summarized for the depth groupings identified from the previous statistical analyses, separating between shallow and medium/deep cavities. Data from the cavity bottoms were excluded since the sediment-covered bottoms were largely devoid of encrusting coelobites. Algal cover decreased with decreasing light intensities continuously from around 60-75% at the entrance to 0-10% 100 cm inside the cavities. Sponges on the other hand increased from around 10% at the entrance to 25% at the distal end of the cavities. The mixotroph hermatypic corals were responsible for the initial contribution of the scleractinians near the entrance whereas inside only the solitary zooplanktivorous Caryophyllidae occured in considerable numbers. Soft corals were hardly encountered. Polychaetes occurred only in the deeper caves and increased with distance from the cave entrance, where they could reach high densities forming dense crusts.

Discussion

Community composition and diversity

The present study provides the first extensive data set for coelobite communities in narrow coral reef crevices revealing a high density and diversity of sessile organisms. Sponges were by far the most diverse group, constituting almost half of the 274 taxa encountered. They were also the most abundant cryptic animals, accounting for 27% of the total fauna cover. The species list is extensive, yet still incomplete, largely due to the lack of reference material. Identification was difficult on a purely morphological basis, because of similar growth forms, color, etc. between disparate groups, but also because a given species may display quite different phenotypes. The former would tend to underestimate, the latter to overestimate sponge diversity. If we assume that the above number of taxa was a realistic approximation of sponge diversity, then these cavities appear to be very diverse.

In terms of cover, sponges were surpassed only by the flora, which consisted mainly of moderately diverse encrusting red algae. Under the favorable light conditions near the entrances the competitively superior algae may prevent other benthic organisms from settlement. Additional limitations could be due to UV-radiation (depending on depth) that has been shown to be harmful to a range of coelobites (Jokiel 1980), as well as to predation exposure. Away from the entrances algae gave way to sponges and other heterotrophic organisms in the deeper zones of the cavities (Fig. 2). This distinct shift was observed in all caves within 50-75 cm from the cavity entrance. We found neither brachiopods, nor sclerosponges, which were typical for the more remote and dark cave zones in the Caribbean and Madagascar (Hartman & Goreau 1970, Vasseur 1974, Logan 1981). Both groups have been reported only anecdotally from Red Sea caves, e.g. by Jackson et al. (1971) who observed brachiopods in a single cavity at 10 m depth at Ras Mohammed. Sclerosponges are present in the Red Sea but are only rarely encountered (Wörheide, pers. com.).
The investigation revealed coral reef cavities as an important habitat for actively filter feeding sponges and ascidians as well as for passively suspension feeding corals, hydrozoans, etc., emphasizing the importance of cavities in the coral reef ecosystem as sinks for plankton and particulate organic matter as proposed by Richter & Wunsch (1999).

Determining factors for coelobite distribution

In addition to the general zonation, coelobite communities showed significant changes on a small scale due to depth, flushing and light. Depth was the overriding factor shaping the composition of communities. The water motion was much higher in the shallow cavities. Close to the surface the wave action was significant. Data indicate that the water is funneled into the narrow cavities which leads to an accelerated water movement inside them. This certainly has negative consequences for fragile or sensitive organisms or larvae which want to settle there. On the other hand the food supply should be very good. However the factor depth has not only physical properties. The shallow cavities are located in a lagoon-like setting which is quite different to the environment of the medium deep and deep cavities. This may have an additional influence on the coelobite communities as the surrounding fauna and flora is different.
The differences in the communities along the cave axis were best explained by a combination of factors, namely the distance from entrance (DIST), the light gradient and depth. The light gradient was strong, spanning up to four orders of magnitude between the entrance and inner reaches of a given cavity (0.005-16.5%). Light and DIST are naturally highly correlated, but the latter involves additional factors, as e.g. protection from predation (Kobluk 1988). The role of predation on the structure of coelobite communities cannot be addressed on a purely observational basis, calling for additional experiments. On the other hand competition between sessile coelobites,

overgrowth, etc. was high. Disturbance of communities has been regarded as one of the driving forces for their diversity (Connell 1978). We observed many interspecific interferences driving changes which are likely to effect species abundance and diversity. Sponges that were monitored for several weeks, could shrink rapidly, vanish or redirect their orientation of growth (Kötter & Wunsch, unpubl.).

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In situ uptake of ultraplankton by Red Sea cavity-dwelling and epi-reefal sponges

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Abstract

Sponges abound in Red Sea coral reef crevices, yet how these filter feeders manage to meet their nutritional requirements in plankton-depleted waters remains enigmatic. We carried out comparative in situ measurements of ultraplankton (< 10 µm) uptake rates in nine species of Red Sea sponges, belonging to three ecologically distinct groups: obligate coelobites (OC), living exclusively in coral reef crevices; facultative coelobites (FC), occurring both, inside crevices and on the outer reef surface; and epi-reefal sponges (ER), dwelling only on the exposed reef surface. Retention efficiencies, derived from comparisons of inhalant and exhalant waters taken with microsamplers from 2.9±1.1 mm (median±MAD) diameter oscula, differed between plankton groups: the larger eukaryotic algae were retained less efficiently (around 60%) than the smaller autotrophic prokaryotes *Prochlorococcus* and *Synechococcus* (>90%), with no marked differences between sponge groups. The most abundant but smallest plankton fraction, the heterotrophic bacteria, were retained most efficiently by OC (83±6%, median±MAD), albeit at eight-fold lower pumping rates corresponding to the replacement of an equivalent of their body volume once every 7.2±2.6 s (median±MAD). Low volume throughput and high retention efficiency appear as adaptations of OC to the limited supply of plankton in framework crevices. OC and FC community uptake amounted to 0.60±0.36 g C d^{-1} per projected m^2 of reef, equivalent to one sixth of the gross productivity of the entire reef. ER community uptake was more than one order of magnitude lower, compounding the importance of coelobite filter feeders in harnessing pelagic material for the reef benthos.

Introduction

Red Sea coral reefs harbor high densities of filter feeders, albeit hidden within the reef's interior (Richter et al. 2001). Quantitative assessments using novel endoscopic techniques (Wunsch and Richter 1998) unearthed a diverse and biomass-rich assemblage of coelobite (cavity-dwelling) sponges, many of which are new to science. Depletions of phytoplankton and bacteria between near-reef and crevice waters (Buss 1979; Gast et al. 1998; Richter and Wunsch 1999), alongside nutrient enrichments in the crevices (Richter et al. 2001) suggest that the crevice biota play a significant role in supplying plankton-derived allochthonous nutrients to the coral reef ecosystem. However, data on the metabolic activity of coelobite sponges to support this assumption are virtually non-existent, due to the small size and cryptic nature of the specimen.

Here we present the results of a field study comparing the filtering performances of nine Red Sea species of sponges representing 3 different ecotypes: obligate coelobites (OC), found exclusively in framework crevices; facultative coelobites (FC), occurring both, in crevices and on the exposed reef surface; and epi-reefal sponges (ER), not recorded in framework crevices.

Out of the 133 varieties of sponges identified in a previous study (Wunsch et al. in press), the majority (>90%) belongs to FC, suggesting a wide plasticity of these species to very different conditions prevailing in crevices and on the exposed reef, respectively. Of particular interest, however, from the ecological point of view, are those species exclusively confined to framework crevices (OC). These could be relict forms whose once widespread range of distribution has been reduced to small pockets. An example are the coralline demosponges (Sclerosponges), an important class of the fossil sponge fauna, which are represented by few specimen restricted to shaded or cryptic areas of modern reefs (Wörheide et al. in press). Interestingly, however, the most abundant species in Red Sea framework crevices, the demosponge *Chondrilla sacciformis*, is also OC, suggesting a modern species adapted to the unique features of the crevice environment (Richter and Wunsch 1999). As mentioned elsewhere (Richter et al. 2001), the absence of these putatively low-food specialists from the exposed reef indicates either or both, higher susceptibility to predators and competitive inferiority to FC and ER. The absence of ER in crevices, by contrast, may be due to food limitation in coral reef crevices.

The present investigation aims at identifying potential adaptations of OC to the notoriously food-impoverished environment prevailing in framework crevices, and to compare "downstream" traits in coelobite sponges to ER living food-upstream.

Methods

Sponges – The most abundant facultative cryptic (FC) sponges, occurring both on the reef as well as in crevices, were: *Hemimycale arabica, Negombata magnifica* and a gray variety of *Callyspongia* sp. 1. *H. arabica* has several root-like canals radiating from slightly raised excurrent openings, whereas *Callyspongia* sp. 1 has pitted excurrent openings. *N. magnifica* comes in two different morphotypes: in protected habitats it is a thin encrusting sponge with one osculum being larger than the other ones. In exposed locations on the reef, *N. magnifica* grows as an erect, antler-like branching sponge of up to 70 cm height. Branches are round to oval and around 1-3 cm in diameter.

Relatively few species occur only in crevices as obligate coelobites (OC), i.e. *Tethya* aff. *seychellensis*, *Chondrosia* aff. *reniformis* and *Chondrilla sacciformis. T.* aff. *seychellensis* is a red, ball-like sponge that has protostyles for attaching itself to the substrate and a single osculum with septa and distinctive buds. Oscula of *C.* aff. *reniformis* are prominent, and slightly raised. *C. sacciformis* is the most abundant species, individual specimen covering up to a few m^2 of crevice wall. With about 1 mm diameter their oscula are the smallest of all sponge species investigated in this study.

Of the epi-reefal sponges (ER) we investigated three conspicuous regularly occurring species: *Crella cyatophora*, *Mycale* sp. and a brown variety of *Callyspongia* sp. 2 belonging to a different species (van Soest, pers. comm.). *C. cyatophora* has sieve-like areas of tightly packed incurrent pores that surround few protruding excurrent pores whereas *Mycale* sp. has slightly raised excurrent openings and *Callyspongia* sp. 2 has few vein-like canals radiating from protruding oscula. For further descriptions of sponge characteristics see Table 1.

Underwater photographs were taken of all specimen used in the experiments. The images were digitized, the number of oscula counted and total area of the sponge measured by image analysis with the public domain software NIH-Image (http://rsb.info.nih.gov/nih-image/). Sponges were outlined manually with the digitizing pen to calculate the cover (cm^2) of each individual. Body volume (cm^3) was determined by multiplying the areal cover with the thickness of each animal measured with a caliper underwater. We distinguished between two

"morphotypes": all sponges thinner than 1 cm were categorized as "crust" whereas animals exceeding 1 cm thickness with bumpy or convex body shapes were classified as "massive". Dry mass (DM) (24 h at 90°C) and ash-free dry mass (AFDM) (5 h at 450°C) were determined for each specimen.

Experimental design – We determined the in situ feeding rates of the sponges by combining data on the volume flow of water through the oscula with the concentration difference between inhalant and exhalant water samples.

Nine species of coral reef sponges (3 OC, 3 FC, 3 ER) were selected for in situ feeding experiments from different locations at 4-13 m depth in the coral reef reserve in front of the

Marine Science Station Aqaba, Jordan, Red Sea. Experiments were done by SCUBA diving from 25 August to 20 September 2001. Triplicate samples were taken from the exhalant and inhalant currents respectively of three individuals per species, yielding a total of 18 samples per species. Their pumping rate was determined consecutively by macro-videography. Prior to the experiment, pumping activity of the sponges was monitored visually and only fully active sponges were selected.

The sampling set-up (microsampler) consisted of a tripod carrying a 3-D positioning rail allowing exact maneuvering of a custom-built syringe holder mounted on top. The syringe holder accommodated two 5 ml syringes spaced 3.5 cm apart enabling simultaneous sampling of exhalant and ambient water (Fig. 1). For the exhalant waters, the needle of the syringe was positioned directly in the center of the osculum. For the inhalant waters, the needle was positioned near the incurrent ostia 1 cm above the sponge surface. Experiments with fluorescent dyes showed that incurrent water samples were unaffected by exhalant flow. Syringes were filled manually by slowly turning a fine threaded 8 mm screw connected to a piston holder. Thus filling of a set of syringes took about 7 min. To exchange syringes, the syringe holder was turned away from the osculum. Filled syringes were taken out, sealed with a silicone cap and stored in a plastic bag. The holder was refitted with 2 empty syringes and maneuvered back. After collection of water samples, the syringes were taken to the lab and processed within 20 min.

Table 1. Sponges investigated during the study (Min - Max values, n= 3 for all species). AFDM: ash-free dry mass

Sponge species	Code	Ecotype	Morphotype	Color	Thickness (cm)	Oscula diameter (mm)	Sponge surface (cm2)	AFDM (g)
Callyspongiasp. 1	C1	facultative cryptic	crust	gray	0.8 - 1.0	1.5 - 1.8	28.1 - 63.4	1.40 - 3.44
Hemimycale arabica	Ha	facultative cryptic	crust	blue	0.3 - 1.2	2.5 - 4.2	4.3 - 17.5	0.05 - 0.16
Negombata magnifica	Nc	facultative cryptic	crust	red	0.5 - 1.0	1.4 - 2.8	2.4 - 6.1	0.07 - 0.27
Negombata magnifica	Nm	facultative cryptic	massive	red	1.0 - 3.0	2.7 - 4.0	13.9 - 20.4	0.53 - 0.58
Chondrosiaaff. reniformis	Cr	obligate cryptic	massive	dark brown	1.0 - 1.2	2.1 - 2.4	7.6 - 15.6	0.69 - 1.84
Chondrilla sacciformis	Cs	obligate cryptic	crust	light brown	0.2 - 0.3	1.1 - 1.4	21.6 - 357	1.80 - 30.98
Tethyaaff. seychellensis	Ts	obligate cryptic	massive	red	2.8 - 3.5	6.4 - 9.1	24.6 - 38.5	0.79 - 1.28
Callyspongiasp. 2	C2	epi-reefal	crust	brown	0.8 - 1.0	2.4 - 3.3	9.1 - 51.8	0.57 - 3.31
Crella cyatophora	Cc	epi-reefal	massive	beige	1.0 - 5.0	4.4 - 5.9	13.6 - 63.7	0.42 - 2.52
Mycalesp.	Ms	epi-reefal	crust	bright red	0.2 - 0.3	3.5 - 4.1	16.9 - 152	0.18 - 1.53

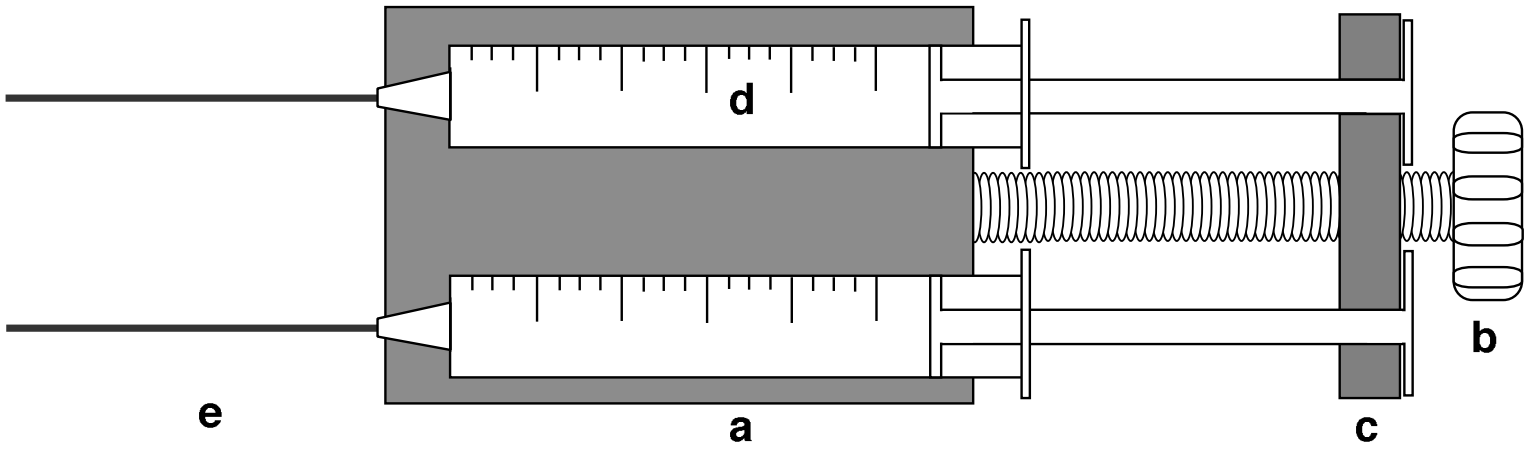

Fig. 1 Syringe holder **(a)** with screw **(b)**, piston holder **(c)**, syringe **(d)** and needle **(e)**.

Pumping rates – After sampling, the stream of water emanating from the osculum was filmed with an underwater video camera (a digital SONY VX1000E in a Sealux housing) mounted on a tripod. The camera axis was parallel to the perimeter of the osculum, perpendicular to the exhalant flow, with the focal plane of the camera on the center of the osculum. The underwater lamp was mounted perpendicular to the axis of the camera, emitting a plane of light on the exhalant flow. Thus particles transported within the exhalant flow became visible and were recorded with the video camera using a macro lens and an open aperture for a narrow depth of field. For calibration of the flow speed a measuring tape was held beside the osculum and recorded. Frame sizes ranged from 13x18 to 19x27 mm. For each osculum 10 particles in the focal plane were selected for analysis. The osculum jet velocity u (cm s^{-1}) was calculated from the number of frames it took a particle to cross a given distance, and a video frame rate of 25 frames s^{-1}. The diameter of each osculum was measured by digital image analysis and its cross-sectional area A (cm^2) calculated.

The flow profile across the oscula was rectangular, not parabolic as in laminar pipe flow (see also Vogel, 1994), in line with Savarese (Savarese et al. 1997) for sponges and Fiala-Medioni for ascidians (Fiala-Médioni 1973, 1978). The osculum flow rate F (cm^3 s^{-1}) was therefore calculated as:

$$F = u \times A \qquad (1)$$

Mass-specific pumping rate P (L g $AFDM^{-1}$ h^{-1}) was calculated as:

$$P = F \times O \times ct \times cv \ / b \qquad (2)$$

where O is the number of oscula cm^{-2} sponge, b is the area-specific biomass of the sponge (g AFDM cm^{-2}) and ct and cv are conversion factors between time and volume units.

Flushing time τ (s) denotes the period of time required by one individual to filter a volume of water equivalent to its own body volume. It was calculated according to the formula:

$$\tau = V / (\sum o \times F) \qquad (3)$$

where $\sum o$ is the number of oscula of one individual, F is the flow rate (cm^3 s^{-1}) and V is the body volume of the sponge (cm^3).

Retention efficiency (RE) for each type of picoplankton was calculated for each sponge species as:

$$RE = 100 \times (i-e) / i \qquad (4)$$

where *i* and *e* are the cell numbers of the respective ultraplankton component from the inhalant and exhalant water sampled from the sponge osculum.

For statistical analysis a one- or two-way ANOVA was performed. Variables were log-transformed when requirements for normality (Kolmogorov-Smirnov test) and/ or homogeneity of variances (Bartlett's test) were not fulfilled. Fisher PLSD or Scheffé tests were used for post-hoc comparisons. When homogeneity of variance could not be achieved with any type of transformation, the Mann-Whitney U test was applied. Percentage data were ARCSINE transformed. For consistency, all results were expressed as median±MAD (median absolute deviation).

Transects – To calculate the epi-reefal cover and biomass of sponges on the upper fore-reef slope of the fringing reef, forty 1 m-quadrates were randomly cast between 7-22 m depth. A separate grid of mesh wire (consisting of 25 squares of 2.5 x 2.5 cm, total area of 156.25 cm^2) was employed to estimate the sponge cover encountered within the 1 m quadrate. Dead and live cover of other reef organisms was also recorded. Biomass was calculated by combining sponge cover with area: biomass-relationships (see above). Coelobite sponge biomass was taken from a previous investigation at the same site (Richter et al. 2001), with OC and FC making up to 12 and 88% of the biomass (Wunsch, unpubl. data).

Sample preservation and analysis – *Prochlorococcus*, *Synechococcus*, heterotrophic bacteria and eukaryotes were analyzed with a FACSort flow cytometer (Marie et al. 2000) at the Station Biologique de Roscoff in France. 2 ml of each sample were preserved with paraformaldehyde solution (1% final concentration) according to standard protocols (Campbell et al. 1994).

To calculate the carbon content of the investigated ultraplankton, we applied the following biomass conversion factors: 20 fg C $cell^{-1}$ for heterotrophic bacteria (Lee and Fuhrman 1987), 53 fg C $cell^{-1}$ for *Prochlorococcus* (Campbell et al. 1994), 250 fg C $cell^{-1}$ for *Synechococcus* (Kana and Glibert 1987) and 2096 fg C $cell^{-1}$ for eukaryotes calculated from the regression pg

C= 0.433 × (body volume)$^{0.863}$ (Verity et al. 1992) and an average cell volume of 6.22 µm^3 (Campbell et al. 1994).

Results

All sponges investigated showed high retention efficiencies (RE) for all ultraplankton groups - up to 99% of suspended cells between inhalant and exhalant waters. RE appear to be related to plankton size, being highest (95.7±1.7%) for the 0.6-1 µm size fraction, represented by *Prochlorococcus* and *Synechococcus* (Fig. 2 a), irrespective of sponge eco- (OC, FC and ER) or morphotype (encrusting and massive growth forms). Larger eukaryotic algae were retained less efficiently (59.4±7.2%) exhibiting differences between sponge morphotypes (two-way ANOVA, F=7.49, df=1, p=0.007) and a combination of morpho- and ecotype (two-way ANOVA, F=4.75, df=2, p=0.012) (Fig. 2 b). In spite of their minute size, heterotrophic bacteria (<0.5 µm) were retained rather efficiently, particularly by OC confined to the inner reef framework (82.6±6%) (Fig. 2 a).

Mass-specific pumping rates (P) were not related to morpho- but to ecotype (one-way ANOVA, F=35.56, df=2, p<0.0001) (Fig. 3 a+b). Those of OC were more than one order of magnitude lower (1.2±0.6 L g AFDM^{-1} h^{-1}) than those of FC and ER, resulting in significantly lower ultraplankton uptake rates (21.6±4.8 µg C g AFDM^{-1} h^{-1}) (Fig. 4). Uptake rates were not significantly different between FC and ER (673.4±401.0 and 569.2±351.2 µg C g AFDM^{-1} h^{-1}, respectively).

Prochlorococcus concentrations were near or below detection in most instances (Table 2). For conservancy, they were omitted in the calculations of total ultraplankton uptake (Table 3).

Oscula jet velocities differed significantly between species (one-way ANOVA, F=23.98, df=8, p<0.0001), being lowest in the two OC species *Chondrosia* aff. *reniformis* and *Chondrilla sacciformis* (4.1±1.4 cm s^{-1} and 2.8±0.3 cm s^{-1}, respectively) (Fig. 5).

Flushing time (τ) was significantly different between morphotypes (Mann-Whitney U, p=0.0017), ecotypes (one-way ANOVA, F=38.5, df=2, p<0.0001) and species (one-way ANOVA, F=150, df=8, p<0.0001). OC filtered the equivalent of their body volume every 7.2±2.6 s, while FC and ER took nearly half as long (Fig. 6 a). Sponges growing as crusts had flushing times of 4.3±2.6 s, whereas massive sponges took 6.8±6 s (Fig. 6 b). Between

Table 2. Cell concentrations (median±MAD) in in- and exhalant currents. Pro: *Prochlorococcus*,Syn: *Synechococcus*,Bac: heterotrophic bacteria, Euk: eukaryotes, For every species triplicate samples were taken from three different oscula of specimen, yielding a total of 90 samples for inhalant and exhalant waters, respectively. •: below detection.

Species	**Inhalant**				**Exhalant**			
	Pro (10^4 cells ml^{-1})	**Syn** (10^3 cells ml^{-1})	**Bac** (10^5 cells ml^{-1})	**Euk** (10^3 cells ml^{-1})	**Pro** (10^4 cells ml^{-1})	**Syn** (10^3 cells ml^{-1})	**Bac** (10^5 cells ml^{-1})	**Euk** (10^3 cells ml^{-1})
Callyspongia sp. 1	14.12 ± 1.50	17.60 ± 2.18	6.20 ± 0.65	2.64 ±0.04	•	0.68 ± 0.15	1.30 ± 0.20	1.14 ± 0.03
Hemimycale arabica	13.22 ± 0.81	26.85 ± 2.54	6.48 ± 0.58	3.21 ± 0.16	•	0.75 ± 0.31	1.78 ± 0.16	1.03 ± 0.20
Negombata magnifica (crust)	12.51 ± 0.45	23.12 ± 1.26	5.41 ± 0.62	2.90 ± 0.49	0.54 ± 0.01	0.77 ± 0.22	1.53 ± 0.16	1.08 ± 0.16
Negombata magnifica (massive)	14.21 ± 23.92	27.38 ± 3.10	6.47 ± 0.73	2.94 ± 0.11	0.53 ± 0.19	0.67 ± 0.03	1.92 ± 0.35	1.18 ± 0.08
Chondrosia aff. *reniformis*	10.44 ± 0.40	22.09 ± 1.50	7.02 ± 0.42	3.45 ± 0.33	0.48 ± 0.02	0.59 ± 0.09	0.82 ± 0.04	1.02 ± 0.17
Chondrilla sacciformis	7.74 ± 0.67	15.10 ± 0.93	5.72 ± 0.41	3.08 ± 0.41	1.70 ± 0.03	1.88 ± 0.92	1.05 ± 0.33	1.51 ± 0.22
Tethya aff. *seychellensis*	8.07 ± 0.77	16.63 ± 4.61	4.76 ± 0.53	2.98 ± 0.82	•	1.28 ± 0.99	1.10 ± 0.30	1.17 ± 0.23
Callyspongia sp. 2	•	8.59 ± 1.35	5.80 ± 0.71	1.66 ± 0.15	•	0.37 ± 0.09	1.28 ± 0.14	0.83 ± 0.09
Crella cyatophora	11.14	20.25 ± 2.39	5.09 ± 0.72	2.87 ± 0.33	•	0.98 ± 0.23	1.55 ± 0.12	0.97 ± 0.07
Mycale sp.	•	20.82 ± 1.03	7.68 ± 0.41	3.02 ± 0.16	•	0.95 ± 0.40	2.41 ± 0.27	1.39 ± 0.23
Average sponge	11.56 ± 2.26	20.55 ± 4.41	6.05 ± 0.96	2.94 ± 0.41	0.54 ± 0.03	0.72 ± 0.24	1.43 ± 0.38	1.12 ± 0.18

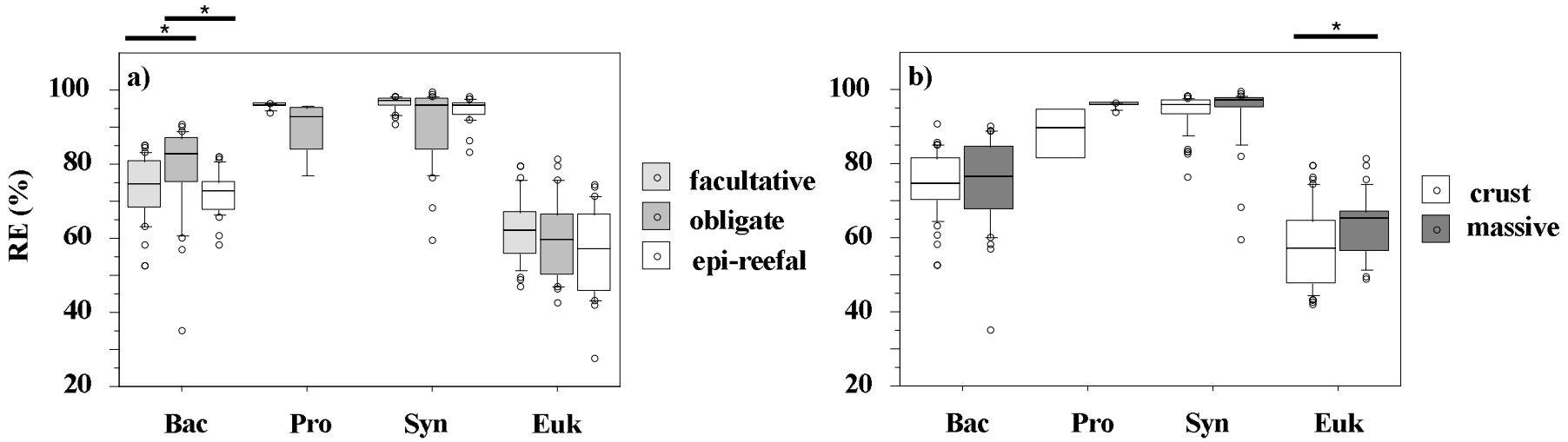

Fig. 2 a+b Median and ranges of retention efficiencies (RE) depending on different ecotype **(a)** and morphotype of sponges (see text for definition) **(b).** Boxes encompass 50% of the data between the 25th and 75th percentile, center lines display the medians. The upper and lower horizontal lines delimit the 10th and 90th percentiles, outliers are shown as open circles. Bars above boxes denote significant differences according toScheffé´s post hoc comparisons **(a)** and Mann-Whitney U test **(b)**, * $p<0.01$.

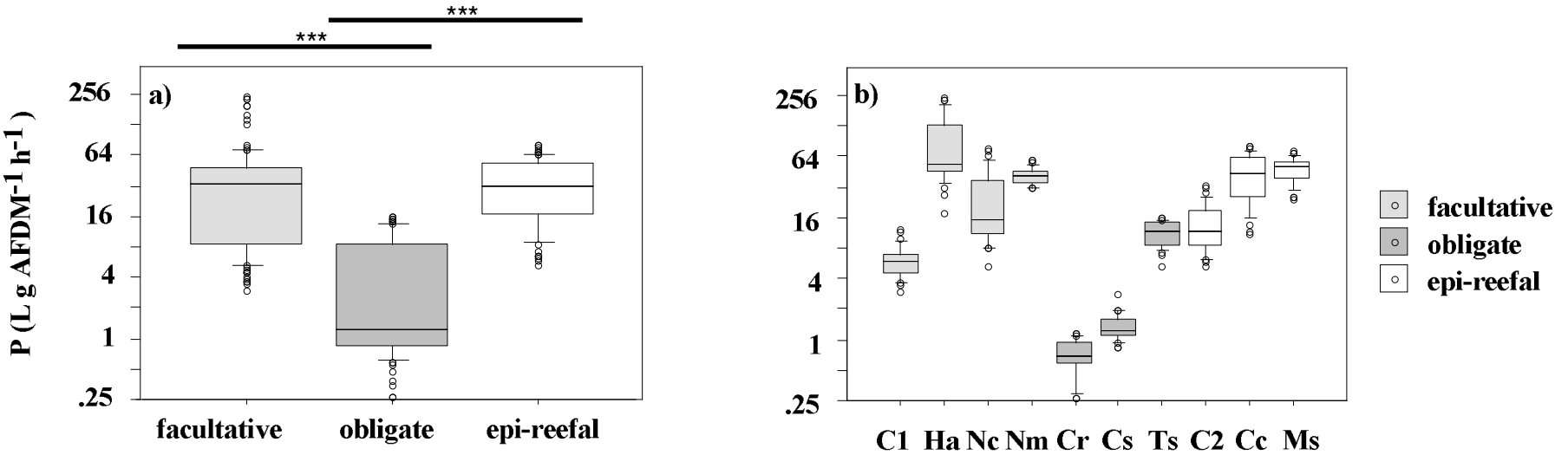

Fig. 3 a+b Median and ranges of mass specific pumping rates (P) between ecotypes **(a)** and species **(b)**. Significance level from Scheffé´s post hoc comparisons, *** $p<0.0001$. For code of sponge species **(b)** see Table 1.

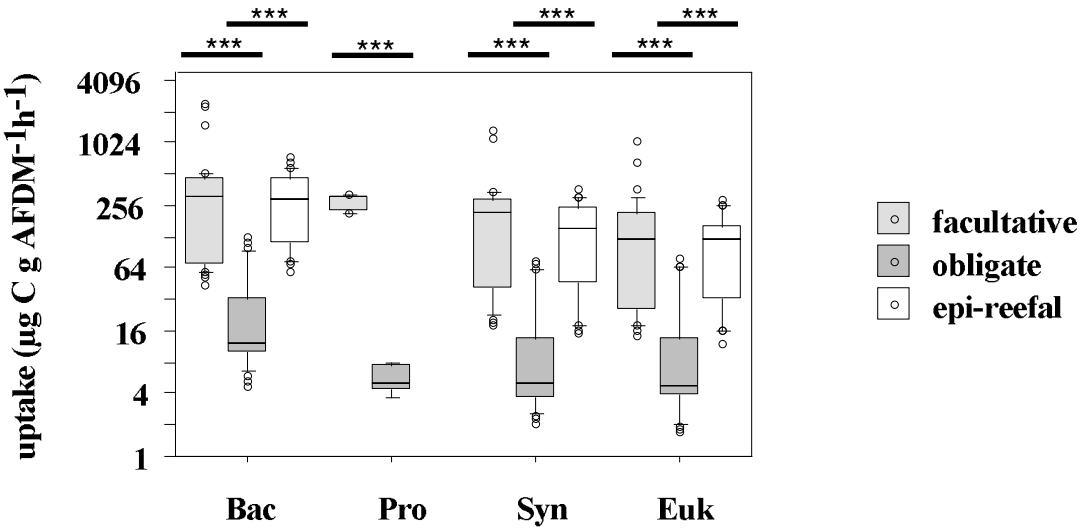

Fig. 4 Median and ranges of ultraplankton uptake depending on the ecotype. Bars above boxes denote significant differences according to Fisher´s post hoc test, *** $p<0.0001$.

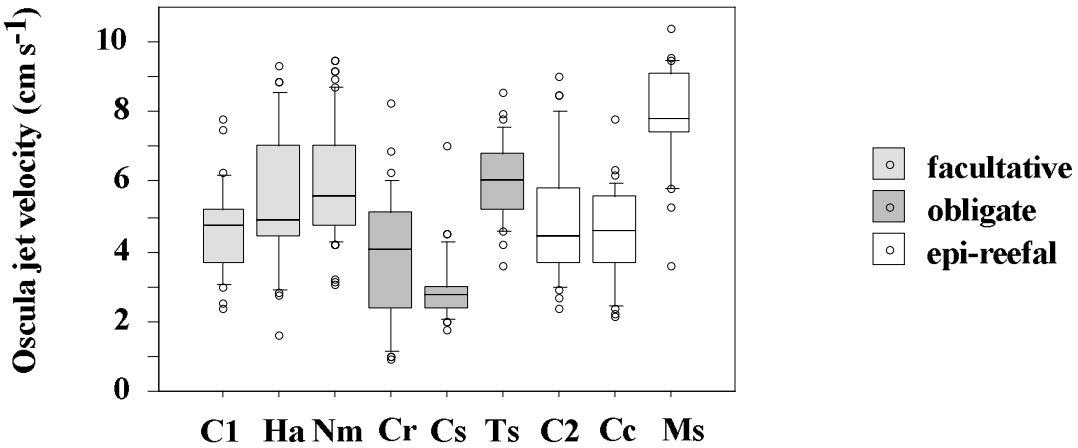

Fig. 5 Median and ranges of velocities measured from the exhalant flow of oscula of all species.

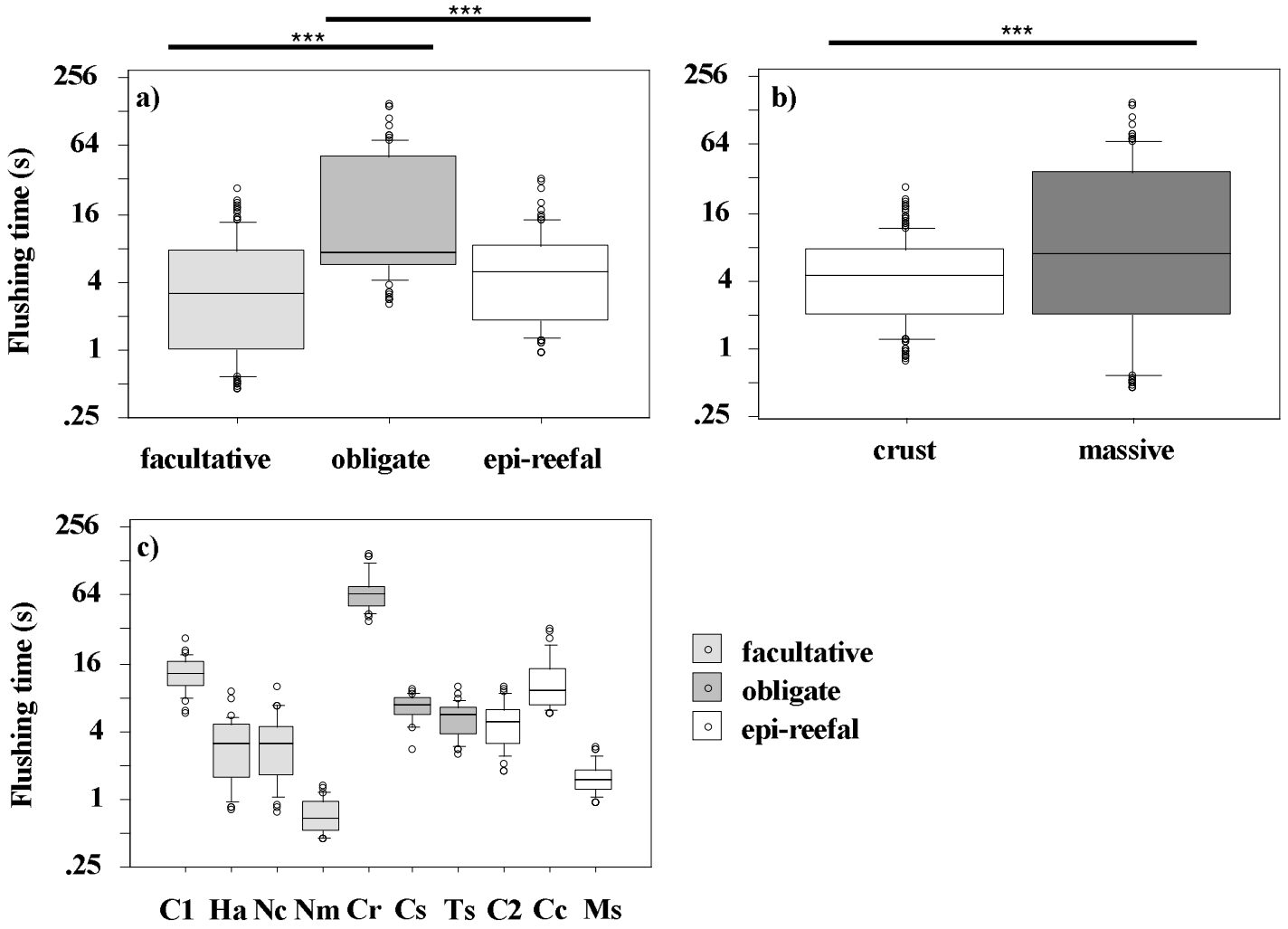

Fig. 6 a-c Median and ranges of flushing times between ecotype **(a)**, morphotype **(b)** and species **(c)**. Significance level according to Fisher´s post hoc test **(a)** and Mann-Whitney U test **(b)**, *** $p<0.0001$. For code of sponge species **(c)** see Table 1.

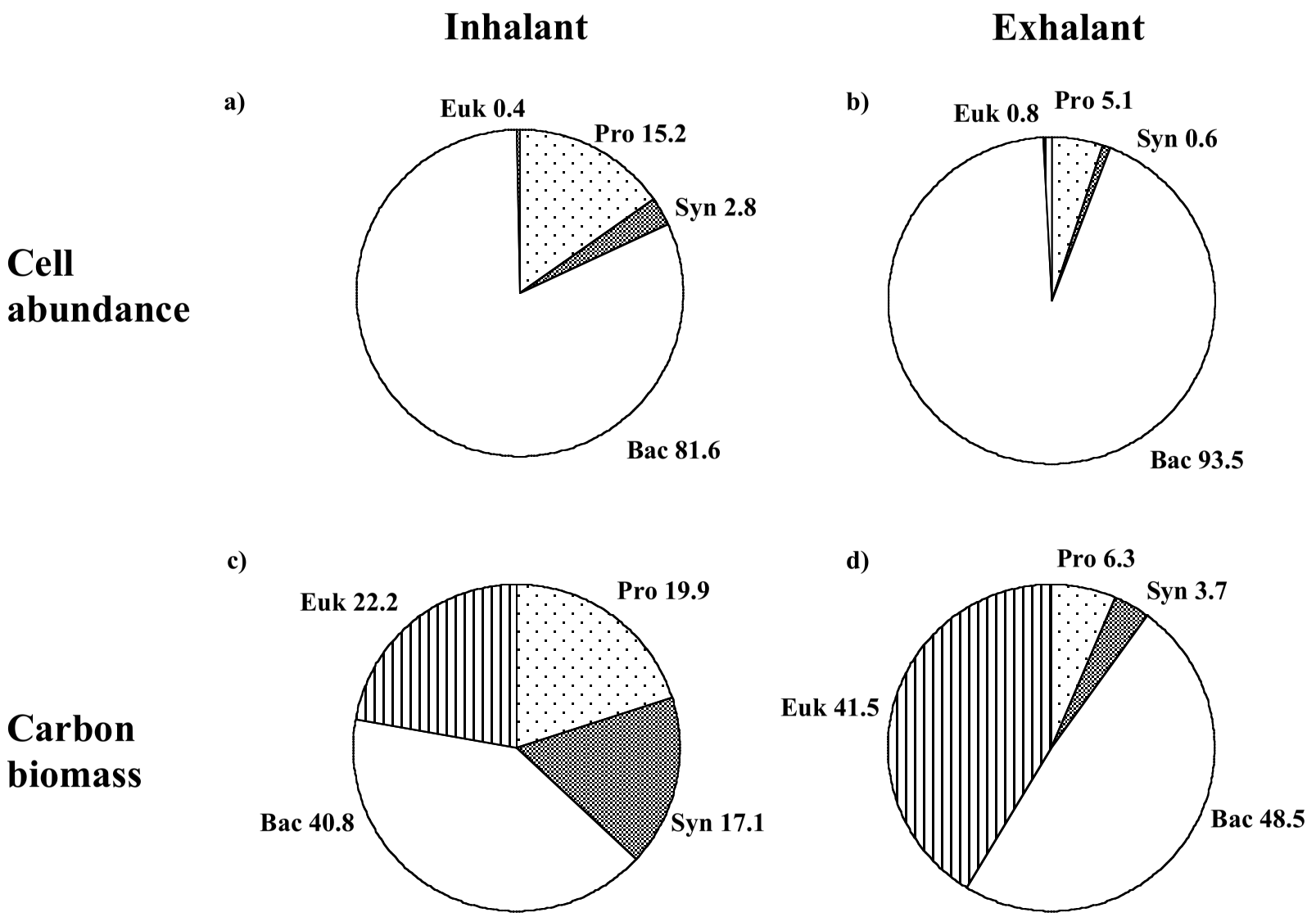

Fig. 7 a-d Ultraplankton composition (%) of inhalant **(a+c)** and exhalant **(b+d)** water samples, depending on cell abundance **(a+b)** and carbon biomass **(c+d)**.
Pro: *Prochlorococcus*, **Syn:** *Synechococcus*, **Bac:** heterotrophic bacteria, **Euk:** eukaryotes. *n*=55 samples

species, flushing times were very variable, ranging from 1.5±0.3 s (*Mycale* sp.) to 64.4±13.3 s (*Chondrosia* aff. *reniformis*) (Fig. 6 c).

Inhalant and exhalant waters differed considerably in their ultraplankton composition (Table 2, Fig. 7 a-d). Whereas total cell numbers decreased by up to more than one order of magnitude after the passage of water through the sponge body, the relative dominance of heterotrophic bacteria increased from >80% to >90%. At the same time, the relative importance of eukaryotic algae increased from 22% to 42% of ultraplankton biomass.

Discussion

Our results suggest that the three distributional groups of sponges indeed represent different ecotypes, which are functionally adapted to the ambient supply of food. As the latter is determined by two factors, volume flow (liters per unit time) and food concentration (e.g. cells per liter), active suspension feeders have two options to adjust their food intake: they may either control the flow of water through their bodies and/or the efficiency of retaining the food particles. Given the low metabolic cost of active suspension feeding (Riisgård and Larsen 1995, 2001; Riisgård et al. 1993), sponges exposed to moderate flow and food concentrations are expected to increase their ration by higher pumping rates, rather than by increasing their retention efficiency. In fact, ER and FC displayed higher pumping rates than OC at the downstream end of the ecotype spectrum, with one ER and FC species replacing an equivalent of their body volume once every <1.5 s. The median flushing time value is well within the range of other sponges (Table 3).

Under conditions of low ambient flow, the cost: benefit ratio for active suspension feeding may become unfavorable (≥1) due to the decreased supply, depletion and reprocessing of food (Vogel 1994). Yet, paradoxically, coelobite sponges constituting the bulk of the Red Sea filter feeders appear to thrive in such low-supply conditions (Richter et al. 2001). They seem to be able to cope with these extreme supply conditions by reducing pumping rates and increasing the retention efficiency, particularly for the smallest particles dominating plankton biomass in coral framework crevices. Enhanced pumping rates would exacerbate refiltration under low-flow conditions.

OC indeed showed >2-fold longer flushing times, with maximal values exceeding one minute (Table 3). They also retained the finest plankton fraction available, <0.5 µm bacteria, most efficiently: up to more than 90% of bacteria were removed from OC exhalant waters,

Table 3. Biomass-specific ultraplankton uptake and pumping rates for sponges and other filter feeders.

Values are median±MAD unless otherwise denoted by symbols. *: arithmetic mean, †: range; #: calculated

Species	Ecotype	Study site	Oscula jet velocity	Flushing time	Pump rate	Mass-specific pumping rate *(P)*	Ultraplankton uptake	Reference
			[cm s^{-1}]	[s]	[cm^3 water cm^{-3} sponge s^{-1}]	[L g $(AFDM)^{-1}$ h^{-1}]	[µg C g $(AFDM)^{-1}$ h^{-1}]	
Sponges (marine)								
Callyspongia sp. 1	FC	Red Sea	4.7 ± 0.9	12.7 ± 2.8	0.08 ± 0.02	5.7 ± 1.2	101 ± 10	this study
Hemimycale arabica	FC	Red Sea	4.9 ± 1.3	3.1 ± 1.4	0.32 ± 0.1	54 ± 16.2	931 ± 217	this study
Negombata magnifica (crust)	FC	Red Sea	5.9 ± 1.3	3.0 ± 1.4	0.33 ± 0.2	14.7 ± 6.0	268 ± 107	this study
Negombata magnifica (massive)	FC	Red Sea	5.4 ± 0.6	0.7 ± 0.2	1.5 ± 0.4	39.8 ± 5.2	893 ± 93	this study
Chondrosia aff. *reniformis*	OC	Red Sea	4.1 ± 1.4	64.4 ± 13.3	0.02 ± 0.01	0.7 ± 0.3	17 ± 3	this study
Chondrilla sacciformis	OC	Red Sea	2.8 ± 0.3	6.8 ± 1.2	0.14 ± 0.02	1.2 ± 0.2	20 ± 2	this study
Tethya aff. *seychellensis*	OC	Red Sea	6.0 ± 0.8	5.5 ± 1.1	0.18 ± 0.03	11.6 ± 2.9	128 ± 74	this study
Callyspongia sp. 2	ER	Red Sea	4.4 ± 1.0	4.9 ± 1.7	0.21 ± 0.09	11.5 ± 5.2	115 ± 15	this study
Crella cyatophora	ER	Red Sea	4.6 ± 1.0	9.2 ± 3.3	0.11 ± 0.04	41.7 ± 18.2	569 ± 165	this study
Mycale sp.	ER	Red Sea	7.8 ± 1.1	1.5 ± 0.3	0.69 ± 0.14	49 ± 8.5	928 ± 127	this study
Mycale lingua		North West Atlantic	14 ± 9.7 *					Pile et al. 1996
Verongia fistularis		West Atlantic	10.2 ± 0.2 *	8.3 #	0.12 ± 0.01 *	4.3 ± 0.3 *#	64 ± 9 *#	Reiswig 1981
Mycale sp.		Caribbean	7.3 ± 0.2 *	4.2 #	0.24 ± 0.01 *			Reiswig 1974
Tethya crypta		Caribbean	14.6 ± 0.2 *	7.1 #	0.14 ± 0.01 *			Reiswig 1974
Verongia gigantea		Caribbean	11.1 ± 0.9 *	11.1 #	0.09 ± 0.01 *			Reiswig 1974
Ulosa ruetzleri, Halisarca caerula, Clathria raraechelae, Merlia normanni	FC	Caribbean					100 ± 63 #	Kötter & Pernthaler in press
Desmanthus incrustans, Diplastrella megastellata	OC	Caribbean					7 ± 3 #	Kötter & Pernthaler in press
Polymastia croceus		South Pacific	84.5 ± 4.8 *					Bell et al. 1999
Dysidea avara		Mediterranean					10 - 183 †	Ribes et al. 1999
Sponges (freshwater)								
Baikalospongia bacillifera		Lake Baikal	1.9 ± 0.9 *	17 - 24 †	0.04 - 0.06 †			Savarese et al. 1997
Spongilla lacustris		Mud pond		6.7 *#	0.15 *#			Frost 1976
Ascidians								
Halocynthia papillosa		Mediterranean					1305 ± 496 *	Ribes et al. 1998

compared to an average 75% by the other groups (Fig. 2 a). Given the fact that bacteria are the dominant particulate source of food in coral reef crevices (Buss and Jackson 1981; Gast et al. 1998), even modest increases in retention efficiencies offer a significant competitive edge to OC filter feeders.

The occurrence of very high densities of associated bacteria in the OC sponges investigated (Kötter and Schumann-Kindel, unpubl.) suggests that, in addition to small bacteria, dissolved organic substances may be assimilated by the sponge-bacterial consortia. Such dietary supplements, already postulated by Reiswig (1974, 1981) and Wilkinson and Garrone (1980), would offer another competitive advantage, particularly to coelobites.

The ultraplankton uptake rates by FC, ER and OC are well within the range of values reported in the literature. Outliers (e.g. the ascidian *Halocynthia papillosa* exhibiting the highest uptake rate of all species listed in Table 3) may be due to methodological differences (e.g. the fact that plankton <100 µm was investigated, whereas our study was restricted to plankton <10 µm). The only reported values from coelobite sponges from the Caribbean (Kötter, in press) did not take into account eukaryotes, and may thus not deviate substantially from our Red Sea findings.

In spite of the low and moderate individual ultraplankton uptake rates for OC and FC sponges, respectively, high OC and FC biomass (21.1 g C m^{-2}, Richter et al. 2001) contributed to high bulk community uptake rates for coelobite sponges (FC and OC), amounting to 0.60±0.36 g C m^{-2} d^{-1}. This figure is in close agreement with independent estimates based on flow speed and concentration differences between crevices and free-stream waters, using a flow respirometric approach (0.7-0.9 g C m^{-2} d^{-1}, Richter and Wunsch 1999; Richter et al. 2001). By contrast, community uptake of ER, covering 0.6 g sponge C m^{-2} reef (this study), was more than one order of magnitude lower (0.02±0.01 g C m^{-2} d^{-1}). Our findings underscore the importance of coelobite sponges for the accrual of oceanic plankton for Red Sea, and possibly other coral reefs throughout the tropics (Ayukai 1995; Glynn 1973; Yahel et al. 1998).

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In situ feeding rates of obligate and facultative coelobite (cavity-dwelling) sponges in a Caribbean coral reef

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Abstract An *in situ* enclosure experiment was carried out to determine the diet and feeding rates of six species of coelobite (cavity-dwelling) sponges in a Caribbean coral reef. The objective of the study was to test whether food-scarcity in coral reef cavities favours filter efficiency in coelobite filter feeders. Facultative coelobite (FC) sponges occurring both, inside crevices and on the outer reef surface had higher filtering rates than obligate coelobites (OC), dwelling exclusively in cavities. Filtering rates in the FC *Clathria raraechelae, Halisarca caerula, Merlia normani* and *Ulosa ruetzleri* averaged 33 µg C cyanobacteria (g ash-free dry weight [AFDW]) $^{-1}$ h^{-1} and 71 µg C bacteria g AFDW^{-1} h^{-1}, depleting 60% of the available carbon. The two most common species of the five OC sponges present in the reef, *Desmanthus incrustans* and *Diplastrella megastellata* were selected for feeding experiments. They removed 5 µg C cyanobacteria g AFDW^{-1} h^{-1} and 16 µg C bacteria g AFDW^{-1} h^{-1}, which corresponds to 20% of the available carbon. The low filtration rates at low ambient food concentrations indicate that OC sponges might acquire carbon from other sources than grazing.

Keywords Coelobites, Suspension feeding, Grazing rate, Sponges, Caribbean

Introduction

Little is known about coral reef cavities let alone the biology of its cryptofauna. Yet, cavities are an important and ubiquitous feature of coral reefs constituting between 30 and 75% of its bulk volume and up to 75% of its total surface (Ginsburg 1983; Kobluk and van Soest 1989). The biomass of cryptofauna may be equivalent or even exceed that of animals living on the outer reef surface (Meesters et al. 1991; Wunsch et al. 2000) as cryptofauna covers up to 95% of the available surface of small crevices and larger caves (Buss and Jackson 1979; Scheffers et al. 2000; Wunsch et al. 2000). Hence competition for food and space is intense (Buss 1979; Buss and Jackson 1981). Although crevices and large caves are dominated by cryptic suspension feeders (Vasseur 1977; Buss and Jackson 1981; Wunsch et al. 2000) little is known about the autecology of these organisms. By use of the CaveCam -an endoscopic video camera system (Wunsch and Richter 1998)- it was shown that sponges are dominant within the cryptofauna, covering up to 50% of the inner cavity walls (Scheffers et al. 2000; Wunsch et al. 2000).

Richter and Wunsch (1999) found intense filtering of phytoplankton in cavity holes, with Chl *a* depletions as high as 86% in the outer meter of a cavernous reef framework, corresponding to a total consumption of 0.7 g C m^{-2} d^{-1}. This rate is much higher than what has been reported for epireefal communities (0.09 g C m^{-2} d^{-1}, Ayukai 1995); it furthermore stresses the importance of cryptofauna as a sink for carbon, a pathway that has been neglected until recently in calculations of reef trophodynamics.

It also gives rise to the question how cryptic animals manage to survive in this food impoverished environment and if they have evolved adaptations to do so. To test for potential differences of feeding efficiency, we compared the feeding rates of OC sponges -occurring exclusively in cavities- to those of FC sponges that dwell both inside the crevices as well as on the outer reef surface.

Methods

Experimental design

Sponges for feeding experiments were collected from the reef at Slaagen Bay (12 km west of Willemstad), on the island of Curaçao, Netherlands Antilles, between February and April 1999. Individual specimen of common OC (4 species) and FC (2 species) sponge species were chiselled off the rock between 15 and 25 m depth. Attached substrate not covered by the sponge was scraped clean of epibionts. Sponge samples were transferred into a wire cage to protect them from predation and stored for recovery in a cavity underneath a coral head at 15 m depth for 7-12 days. Prior to the experiment, pumping activity of the sponges was monitored visually and only fully active sponges were selected for the experiments. Sponges were transferred into 1.2 l glass chambers, filled with ambient seawater and the glass lid was sealed with a silicon ring. Four replicates of each species and two glass chambers filled with ambient water for controls were left in a shaded part of the reef at 15 m depth for 90 minutes. Two ambient water samples were taken at the

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beginning of the experiment to test for effect of enclosure and immediately fixed (T_o). Another two experimental chambers stocked with cleaned bare rock served as controls to test for potential effects of the rock, which proved to be insignificant. After 90 min of incubation (T_1) all chambers were taken ashore. The sponges were removed from the experimental chambers and water samples for oxygen measurements and bacterial counts were fixed immediately. All samples were then stored in a shaded box, packed on ice and transported immediately to the laboratory at the CARMABI Foundation (Caribbean Research and Management of Biodiversity) where they were processed within 3 hours of collection.
Sponge-free control vessels showed no significant differences in bacterial numbers between T_o and T_1 and were pooled for subsequent statistical analysis.

Sample preservation and analysis

For counts of heterotrophic bacteria, 5 ml were preserved with formaldehyde solution (2% final concentration), kept dark and cold for less than 30 min and then frozen at -20°C. Bacterial abundances were analysed by flow cytometry. Samples were double stained with SYPRO red (in excessive concentration, 1/10.000 dilution of the commercial stock) (Molecular Probes, Eugene, Oreg.), a dye which binds to the protein surface, and Hoechst 33342 (final concentration 0.4 µg ml^{-1}) (Molecular Probes), a DNA specific fluorochrome, in the presence of 0.04% SDS (Sodium dodecyl sulphate) at 20°C for at least 15 min (Zubkov et al. 1999).
Yellow-green fluorescent latex microspheres (Molecular Probes) of 0.5 µm diameter were used for alignment of the flow cytometer. Samples were analysed with a FACStar Plus flow cytometer (Becton Dickinson, Mountain View, Calif.) equipped with two lasers. The first, argon laser (Innova 90, Coherent Inc., Palo Alto, Calif.) was tuned to UV multiline-emission (351.1 to 363.8 nm) at 110 mW. The second, diode-pumped solid-state laser (DPSS 532, Coherent), emitted at 532 nm with 200 mW output power. Light that was emitted by the first laser and scattered by particles in the forward direction, was focused through a 360±20 nm band-pass filter onto a photomultiplier tube. A 460±25 nm band-pass filter collected the blue fluorescence from the Hoechst stain whereas a 620±60 nm band-pass filter collected the fluorescence from the SYPRO red, which was excited by the second laser. Data acquisition and cell counts were done with Cell-Quest software (Becton Dickinson). Sample size for analysis was chosen to provide more than 4000 DNA-positive events per sample.
For quantification of cyanobacteria and calculation of cell sizes of heterotrophic bacteria, 40 ml of water was fixed with formaldehyde solution (2% final concentration). 10 ml subsamples were stained with DAPI (4´,6´-Diamidino-2-Phenylindole) and filtered onto black polycarbonate filters (pore size 0.2 µm). A minimum of 400 cells of cyanobacteria or a maximum of 100 grids were counted by epifuorescence microscopy on a Zeiss Axioscope 1 with a 40x Plan Neofluar objective. To calculate the carbon content, a biomass conversion factor of 470 fg C per cyanobacterial cell was applied (Campbell et al. 1994). The length and width of >6000 heterotrophic bacterial cells were measured by semi-automated image analysis (MetaMorph 3.5, Universal Imaging) (Posch et al. 1997) after DAPI staining to calculate a mean cell volume (0.032±0.01 μm^3). The cellular carbon content (CC) was calculated according to the formula: $CC=218 * V^{0.86}$ (V= bacterial cell volume [μm^3]) (Loferer-Krößbacher et al. 1998) resulting in an average carbon content of 11.3±2.0 fg C per heterotrophic bacterium.
For Chl *a* measurements, 3 replicates of 100 ml water samples were filtered onto 25 mm diameter GF/F filters (pore size 0.7 µm, Whatman). The pigments were extracted in 90% acetone for 24 h at 4°C in the dark and measured with a fluorometer (Turner designs Mod. 10-AU-005) using the acidification method (Parsons et al. 1984). We used a conservative C-to Chl *a* conversion factor of 60 (Legendre et al. 1988). Oxygen was measured by Winkler titration (Grasshoff et al. 1976). All sponges morphologically represented thin crusts of 1-3 mm thickness, except *Ulosa ruetzleri* (up to 10 mm). Underwater photographs were taken of all sponges. The images were then digitized and their area was measured by image analysis with the public domain software NIH-Image (http://rsb.info.nih.gov/nih-image/). Sponges were outlined manually with the digitising pen in order to calculate the cover (cm^2) of each individual. Bodyvolume (cm^3) was determined by multiplying the cover with the thickness of each animal. Dry weight (DW) (24 h at 90°C) and AFDW (5 h at 450°C) were determined for each specimen. Retention efficiency (RE) was calculated as the proportion of particles captured at the filtration surface in relation to the total number of particles approaching it (Reiswig 1971a). AFDW specific clearance rate (CR) was calculated by assuming exponential growth and clearance of prey as described by Ribes et al. (1998).
For statistical analysis a one-way ANOVA was performed. Variables were log-transformed when variances were not homogenous and Scheffé tests were used for post-hoc-comparisons.

Results

In all experiments phytoplankton, heterotrophic bacteria and cyanobacteria were significantly depleted (one-way ANOVA, $p<0.05$) by all sponge species, as compared to controls (Table 1). For all experiments and prey types, the percentage decrease during the incubations ranged from 7-88%.
During the experiments the oxygen concentration never dropped below 20% of the initial concentration, staying well above the critical threshold affecting the behaviour and physiology of the sponges (Crisp 1984). The respiration rates of OC sponges (4.7±1.3 mg O_2 g $AFDW^{-1}$ h^{-1}) were not significantly different from those of FC sponges (7.3±4.9 mg O_2 g $AFDW^{-1}$ h^{-1}), (one-way ANOVA, $F=0.01$, df=1, $p=0.9$).
On average FC sponges reduced twice as much Chl *a* (62±49 µg C g $AFDW^{-1}$ h^{-1}) than OC sponges (23±16 µg C g $AFDW^{-1}$ h^{-1}). Due to the large scatter, those differences were not statistically significant ($F=3.3$, df=1, $p=0.08$).
Heterotrophic bacteria were the most important picoplankton fraction, contributing an average of 73.2% to the total picoplankton carbon biomass, whereas cyanobacteria represented only 26.8% of picoplankton carbon. Consumption of heterotrophic bacteria ($F=7.2$, df=1, $p=0.013$) and cyanobacteria ($F=5.1$, df=1, $p=0.0002$) were significantly different between FC and OC sponges. FC sponges consumed four times more bacterial carbon from heterotrophic bacteria (71±66 µg C g $AFDW^{-1}$ h^{-1}) and six times as much from cyanobacteria (33±34 µg C g $AFDW^{-1}$ h^{-1}) as OC sponges (16±17 and 5±1 µg C g $AFDW^{-1}$ h^{-1} respectively).

Table 1 Initial prey and oxygen concentration values for the six different cryptic sponge species (Mean ± SD).
RE: Particle retention efficiency (Minimum-Maximum), % change: percentage of decrease in oxygen concentration of the final water samples with respect to initial concentrations, concentration values: Mean ± SD.

Sponge species	Chl *a* ($\mu g\ l^{-1}$)	R E (%)	Heterotrophic bacteria (10^5 cells ml^{-1})	R E (%)	Cyanobacteria (10^3 cells ml^{-1})	R E (%)	O_2 ($mg\ l^{-1}$)	% change (Min-Max)
Ulosa ruetzleri	0.25 ± 0.02	39-60*	3.3 ± 0.4	47-75*	4.9 ± 1.1	46-69*	4.1 ± 0.1	3-19
Halisarca caerula	0.21 ± 0.01	31-45*	9.2 ± 1.4	83-94*	10.7 ± 2.6	87-97*	6.9 ± 0.1	5-12
Clathria raraechelae	0.25 ± 0.02	28-47*	7.9 ± 0.6	32-71*	8.1 ± 0.6	31-83*	7.2 ± 0.1	8-19
Merlia normani	0.26 ± 0.01	20-45*	9.9 ± 0.4	22-53*	4.9 ± 0.6	33-68*	6.9 ± 0.4	6-7
Desmanthus incrustans[1]	0.19 ± 0.01	8-27*	6.8 ± 0.5	11-17*	2.8 ± 0.7	41-57*	6.6 ± 0.1	7-15
Diplastrella megastellata[1]	0.19 ± 0.00	17-45*	6.7 ± 0.6	18-61*	3.1 ± 0.7	13-54*	6.8 ± 0.1	4-10

[1] obligate cryptic sponge, * significant at $p<0.05$

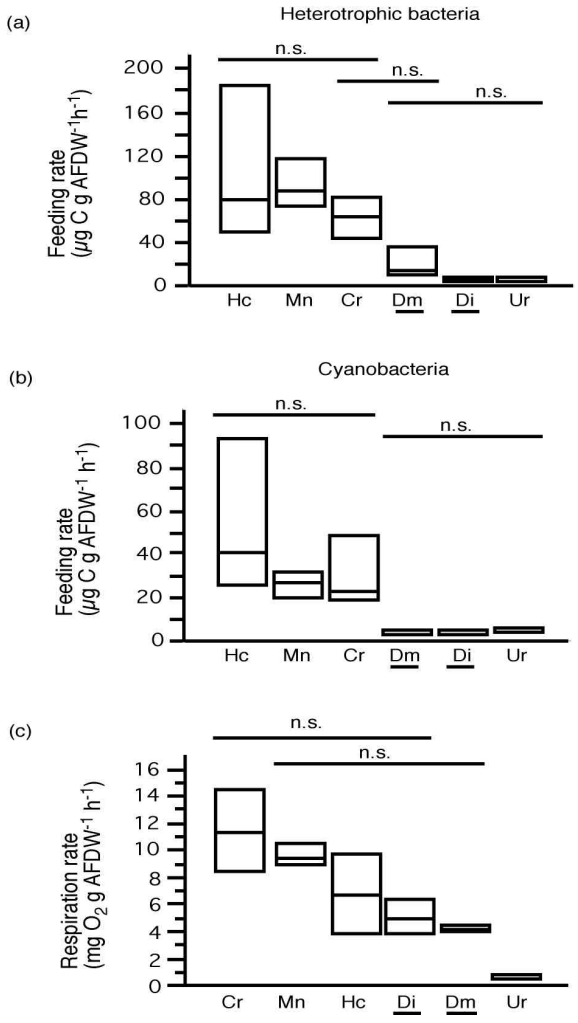

Fig. 1 Median and ranges of differences in feeding and respiration rates after ANOVA ($p<0.05$) and Scheffes´ post-hoc test ($p<0.05$), n.s.= non-significant; Hc*: Halisarca caerula*, Mn: *Merlia normani*, Cr: *Clathria raraechaelae*, Dm: *Diplastrella megastellata*, Di: *Desmanthus incrustans*, Ur: *Ulosa ruetzleri*. Underlined species are obligate sponges.

Therefore the average feeding rate of FC sponges (110±98 µg C g $AFDW^{-1}$ h^{-1}) on the total picoplankton was seven times higher than that of OC sponges (15±4 µg C g $AFDW^{-1}$ h^{-1}). Retention efficiencies of sponge species are shown in Table 1. A one-way analysis of variance for differences in specific feeding and respiration rates (Table 2) showed significant differences between sponge species (Fig.1). Scheffé post-hoc tests were used to group species that did not differ significantly in their feeding and respiration rates (horizontal bars in Fig. 1). A graph for Chl *a* was omitted because there were no overall significant differences between the species (Table 2). AFDW of sponges was significantly correlated with DW (Spearman Rank Order Correlation, $R_S=0.97$, $n=24$, $p<0.01$). The correlation between AFDW and body volume ($R_S=0.83$, $n=24$, $p<0.01$) was higher than with sponge cover ($R_S=0.43$, $n=24$, $p<0.05$).

Table 2 One-way ANOVA for differences in specific feeding and respiration rates of all sponge species for individual prey types.

	df	SS	MS	F	p
Chlorophyll *a*	5	1.535	0.307	1.72	0.18
Heterotrophic bacteria	5	5.212	1.042	18.4	0.0001
Cyanobacteria	5	4.231	0.846	17.2	0.0001
Total picoplankton	5	4.867	0.973	25.2	0.0001
Oxygen	5	3.470	0.694	30	0.0001

Mean specific clearance rates of FC and OC sponges were significantly different for heterotrophic bacteria ($F=4.8$, df=1, $p=0.04$) but not for cyanobacteria ($F=3.8$, df=1, $p=0.06$). Mean specific clearance rates of FC sponges for heterotrophic bacteria were 11451±12083 ml g $AFDW^{-1}$ h^{-1} whereas OC sponges cleared only 2396±3852 ml g $AFDW^{-1}$ h^{-1}. The FC sponge *Halisarca caerula* had the highest clearance rate for both types of bacteria (Table 3). In contrast the OC sponge *Desmanthus incrustans*, that had a similar body weight and larger surface cover, had the lowest specific clearance rate for heterotrophic bacteria (Table 3).

Table 3 Specific clearance rates and sizes of cryptic sponges (Mean ± SD).
CR het B.: clearance rate for heterotrophic bacteria, CR Cyan: clearance rate for cyanobacteria.

Sponge species	Body weight (g AFDW)	Sponge cover (cm^2)	Body volume (cm^3)	CR het B. (ml g $AFDW^{-1}$ h^{-1})	CR Cyan (ml g $AFDW^{-1}$ h^{-1})
Ulosa ruetzleri	0.32 ± 0.2	23.7 ± 12	23.7 ± 12	3141 ± 1413	3728 ± 1415
Halisarca caerula	0.1 ± 0.07	22.7 ± 6.3	6.8 ± 1.9	24976 ± 18629	34783 ± 24630
Clathria raraechelae	0.07 ± 0.05	18.6 ± 10	5.6 ± 3	7550 ± 1552	14606 ± 11773
Merlia normani	0.04 ± 0.01	17.7 ± 4.8	1.8 ± 0.5	10137 ± 4477	15528 ± 7520
Desmanthus incrustans[1]	0.11 ± 0.02	36.8 ± 5.9	7.4 ± 1.2	608 ± 492	5012 ± 1182
Diplastrella megastellata[1]	0.08 ± 0.03	25 ± 10.2	5 ± 2	3749 ± 4872	3205 ± 1154

[1] obligate cryptic sponge

Discussion

Sponges are active suspension feeders which primarily forage on picoplankton (Reiswig 1971a; Huysecom et al. 1988; Reiswig 1990; Van de Vyver et al. 1990; Pile et al. 1996). Gast et al. (1998) discovered significant reductions in bacterial numbers as well as enhanced bacterial growth in small scale coral reef crevices of Curaçao, postulating the importance of cryptic filter feeders in filtering and remineralizing the picoplankton food.

Therefore, we investigated cyanobacteria and heterotrophic bacteria as food items for OC and FC sponges.

For cryptic sponges REs were as high as 97% for cyanobacteria and 94% for heterotrophic bacteria. This is comparable to REs of 89% for *Synechococcus*-type cyanobacteria and 74% for heterotrophic bacteria measured in the boreal marine sponge *Mycale lingua* (Pile et al. 1996), and higher than those found for freshwater sponges from Lake Baikal (58-66% for *Synechococcus*-type cyanobacteria, 71-84% for heterotrophic bacteria, Pile et al. 1997).

In other coral reef sponges REs were as high as 99% for bacteria (Reiswig 1971a; Wilkinson 1978) and 58-99% for different types of picoplankton in freshwater and temperate marine sponges (Van de Vyver et al. 1990; Riisgård, et al. 1993). The OC sponge *Desmanthus incrustans* was the only cryptic sponge that had a significantly higher RE for cyanobacteria than for heterotrophic bacteria (Table 1). REs in all other cryptic sponges were similar for both types of picoplankton, which indicates that they did not feed selectively. This agrees with findings of Pile (1997; Pile et al. 1997) and Ribes et al. (1999) who observed non-selective grazing on these types of picoplankton, as well as with results of Reiswig (1971a) who found no differences between retention rates for smaller (0.03 μm^3) and larger (0.15 μm^3) size classes of bacteria. On the other hand active selection between particles of very different sizes, e.g. pico- and nanoplankton has been reported for temperate, tropical and deep sea sponges (Reiswig 1971a; Pile et al. 1996; Turon et al. 1997; Witte et al. 1997; Ribes et al. 1999).

The mean clearance rates (CRs) of cryptic sponges calculated in this study were quite variable both within and between species (Table 3). Except for *Desmanthus incrustans* the mean weight-specific CRs for heterotrophic bacteria were higher in cryptic sponges (Table 3) than those reported for the Mediterranean sponge *Dysidea avara* (1539±1241 ml g $AFDW^{-1}$ h^{-1}, Ribes et al. 1999). This might be due to the fact that sponge size affects CR (Ribes et al. 1999). The weight of the studied cryptic sponges ranged from 0.03-0.62 g AFDW, whereas the Mediterranean species were much bigger, between 0.3-2.3 g AFDW. Reiswig (1974) estimated CRs of 1054-12360 ml g $AFDW^{-1}$ h^{-1} for larger tropical sponge species. These values are within the same order of magnitude as CRs for heterotrophic bacteria and cyanobacteria estimated for cryptic species (Table 3). For a deep-sea sponge of the Norwegian-Greenland Sea, CRs of 5000-9000 ml g $AFDW^{-1}$ h^{-1} were reported (Witte et al. 1997). The high CRs of tropical cryptic sponge species might reflect a compensation for the low food concentrations in the crevices by processing larger amounts of water.

Carbon consumption of sponges range from 29 mg C m^{-2} d^{-1} for boreal marine species (Pile et al. 1996) to 800-1800 mg C m^{-2} d^{-1} for tropical marine (Reiswig 1971b), and 1970 mg C m^{-2} d^{-1} for freshwater species (Pile et al. 1997). All sponges in the above mentioned studies were larger species with a volume of 2-120 l, and a much higher biomass per m^2 of sponge cover. The cryptic sponges investigated in this study depleted 5-373 mg C m^{-2} sponge d^{-1}. This is a surprisingly high consumption, bearing in mind that cryptic sponges form only thin crusts of 1-10 mm thickness, have little volume (0.001-0.04 l) and a low biomass (Table 3).

Thus depletion rates should rather be reported as carbon consumption per mm^3 sponge and the morphological

features and biovolume of the species under study should be reported. Ribes et al. (1999) found differences in carbon ingestion of the Mediterranean sponge species, *Dysidea avara*, depending on the body weight. An animal of 1.6 g AFDW ingested only 10-12 µg C g $AFDW^{-1}$ h^{-1} whereas one of 0.2 g AFDW ingested 169-183 µg C g $AFDW^{-1}$ h^{-1}. Such a correlation was not found for any individual cryptic sponge species in this study, which had varying body weights of 0.02-0.8 g AFDW and ingested between 7-303 µg C g $AFDW^{-1}$ h^{-1}. This is lower than expected regarding the results of Ribes et al. (1999).

Our findings indicate that OC sponges might acquire carbon from other sources than grazing, as their feeding and clearance rates are lower than those of FC sponges. Another reason for low feeding rates might be that OC sponges were exposed to unnaturally high particle densities, as our experiments were performed with surrounding reef water and not with cavity water. Therefore, the offered food supply might have been too high, and might have resulted in a reduced filtering activity.

Another possibility, which has not been investigated yet, might be that the OC sponges harbour symbionts, which contribute to their food supply. A number of symbioses between sponges and macroalgae (Davy et al. 2000), microalgae and bacteria (Wilkinson 1978; Santavy 1985; Diaz 1997; Ritter et al. 2000) have been reported. According to Ritter et al. (2000) the FC sponge *Chondrilla nucula* harbours about 90 different bacterial symbionts. OC sponges might e.g. live in symbiosis with heterotrophic bacteria, which thrive on dissolved organic carbon and this bacterial biomass might be gradually digested by the sponge cells (Sorokin 1995). Such a symbiosis might enable OC sponges to survive in this light and food impoverished environment.

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Associated bacteria of coelobite and epi-reefal sponges in the Gulf of Aqaba, Red Sea

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Significant differences in ultraplankton uptake rates between coelobite (cavity-dwelling) and epi-reefal sponges have raised the question of alternative energy sources supplementing the diet of species with low filtering rates. In this investigation we explore, if an abundant population of associated bacteria could compensate the low feeding rates of coelobite sponges, by harnessing e.g. dissolved organic carbon in plankton-depleted crevice waters.
To address this question, we applied widefield deconvolution epifluorescence microscopy (WDEM) combined with fluorescent *in situ* hybridization (FISH) on several species of sponges (Manz et al. 2000). FISH with rRNA-targeted fluorescent oligonucleotide probes is a staining technique that allows phylogenetic identification and quantification of bacteria without prior cultivation. The WDEM provides serial digital images to calculate bacterial densities in three-dimensions [N (mm^3 sponge)$^{-1}$]. FISH and WDEM were performed at the Center of Earth Sciences at the University of Göttingen..

Sponges belonging to 5 species (4 specimen each) were collected by SCUBA diving in front of the Marine Science Station Aqaba, Jordan, in 4-12 m depth. We differentiated between three ecotypes: obligate coelobite sponges living exclusively in reef cavities, facultative coelobite sponges occurring inside crevices as well as on the outer reef framework and epi-reefal sponges living exclusively on the exposed reef surface.

Freshly collected samples were immersed in a solution of 3.7% formalin and 0.04% glutaraldehyde for 12-24 h at 4-7°C, then washed with 1 x PBS for 6-12 h at 4-7°C and finally stored in a 1:1 mixture (v/v) of 1 x PBS and 96% (v/v) ethanol in the fridge. Sponge pieces of 1 x 1 cm were cut off with a sterile dissecting knife, dehydrated with ethanol and xylene and embedded into paraffin blocks. With a rotary microtome series of 14 µm thick slices were shaved off and mounted on glass slide. The oligonucleotide probe EUB338 specific for the domain *Bacteria* (Amann et al. 1990) was chosen for the *in situ* hybridization in combination with DAPI, a staining dye detecting pro- and eukaryotic DNA.

With the WDEM stacks of 21 images with a z-spacing of 0.5 µm and stacks of 6 optical sections with a z-spacing of 2 µm were obtained for photo reassignment and 3-D image restoration.

The obligate cryptic sponges *Chondrilla sacciformis* and *Chondrosia* aff. *reniformis* show a loose network of sponge tissue interspersed with dense aggregations of associated bacteria (Color plate 1).
Specimen of the facultative coelobite sponge *Hemimycale arabica* were sampled from the exposed reef surface and the inside of a cave, respectively. Whereas sponge cell densities were similar in both individuals, we found striking differences in the associated microflora. The exposed specimen showed very low densities of single bacteria scattered in the mesohyl (Color plate 2). The coelobite specimen by contrast was tightly packed with high densities of bacteria.
The epi-reefal sponges *Crella cyatophora* and *Mycale euplectellioides* featured low densities of associated bacteria within a dense sponge tissue (Color plate 3).

The high densities of bacteria in coelobite sponges support the hypothesis that associated bacteria may provide a competitive advantage to life in plankton-depleted waters (Richter et al. 2001). This assumption is corroborated by the facultative cryptic *H. arabica*, where the specimen growing inside the cave harbors much more associated bacteria than the specimen growing on the outer reef surface. The sponge host may be gardening bacteria capable of taking up dissolved organic carbon and subsequently ingest the bacteria, thus supplementing its diet (Wilkinson & Garrone 1980). The total carbon uptake by coelobite sponges might therefore be much higher than the ultraplankton uptake rates suggest (Chapters 1, 2, 4, 5).
Bacterial associations were also involved to explain “missing carbon” in the metabolism of the Caribbean sponge *Verongia fistularis*, also featuring associated bacteria (20% of the body volume, Reiswig 1981).
In contrast, the higher ultraplankton uptake rates of epi-reefal sponges in combination with small numbers of associated bacteria in their tissue support our hypothesis that sponges living on the outer reef surface have no need of supplementing their diet.

Furthermore there seems to be a correlation between the structure of the mesohyl and the abundance of associated bacteria: species with dense sponge tissue showed low numbers of bacteria whereas those with a loose tissue harbored high numbers of associated bacteria.

Further investigations are needed to quantify total uptake of all carbon sources including dissolved organic carbon in order to validate our findings. It would also be interesting to quantify the number of choanocyte chambers, as they are likely to relate to the ultraplankton uptake capacity of sponges.

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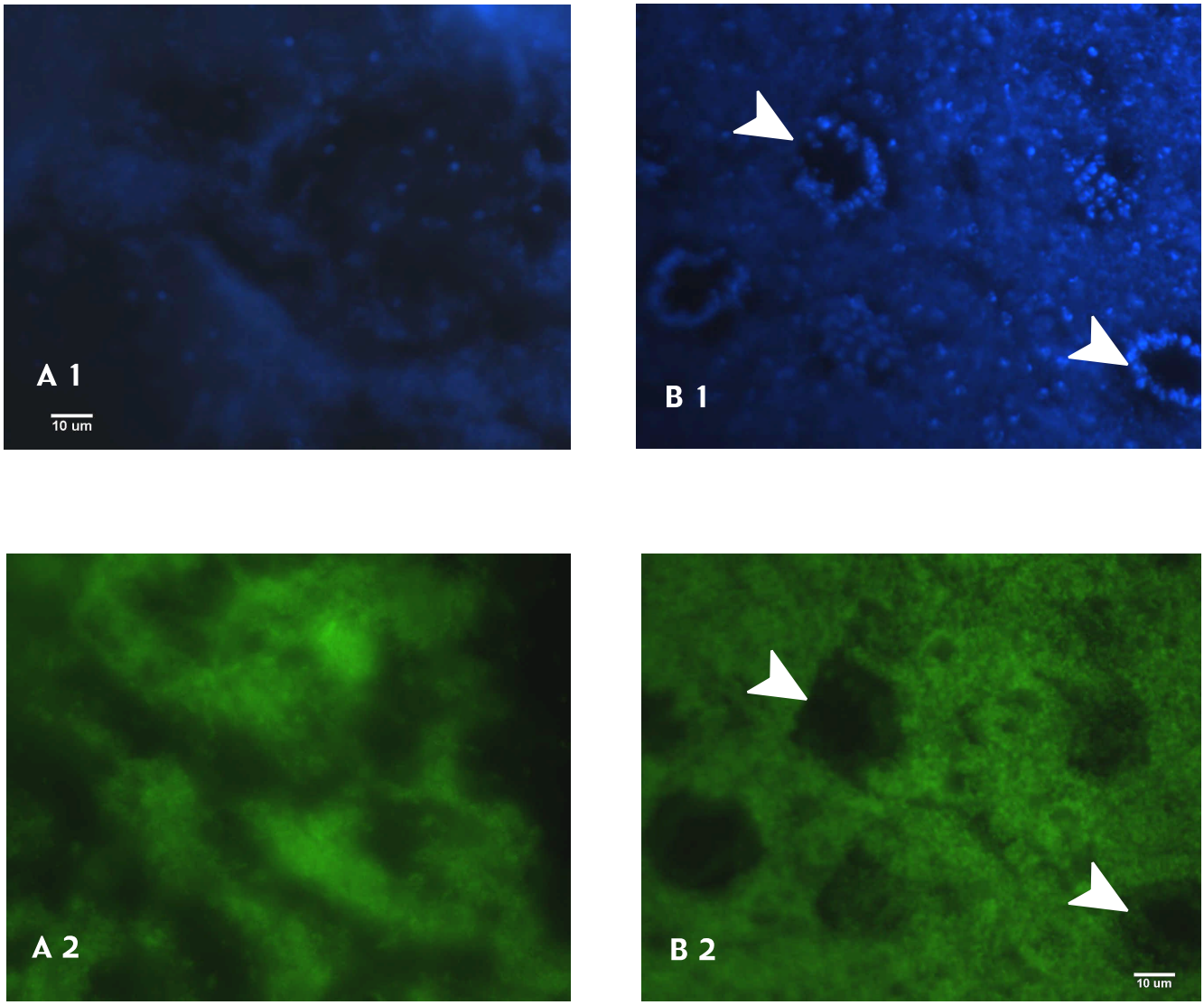
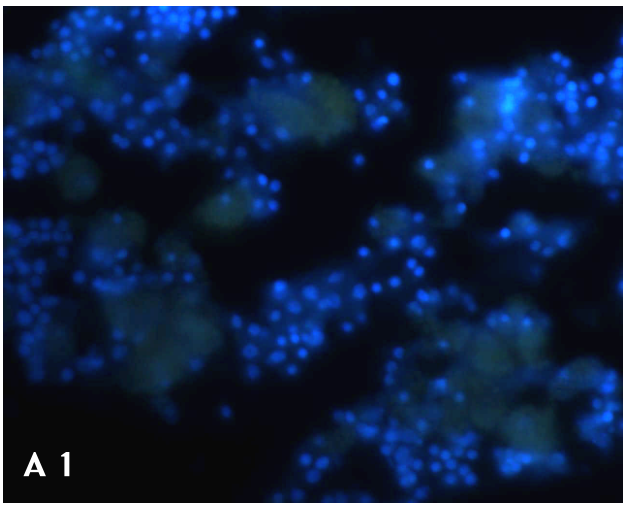
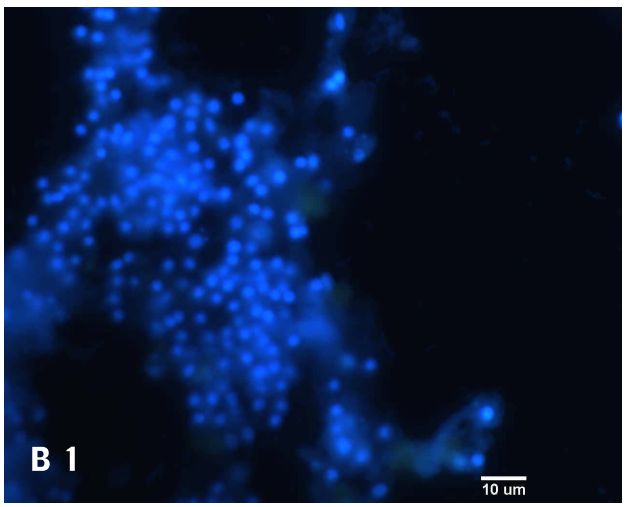
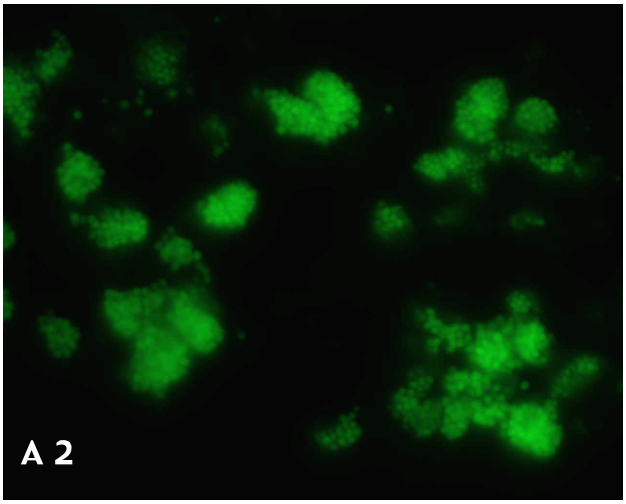
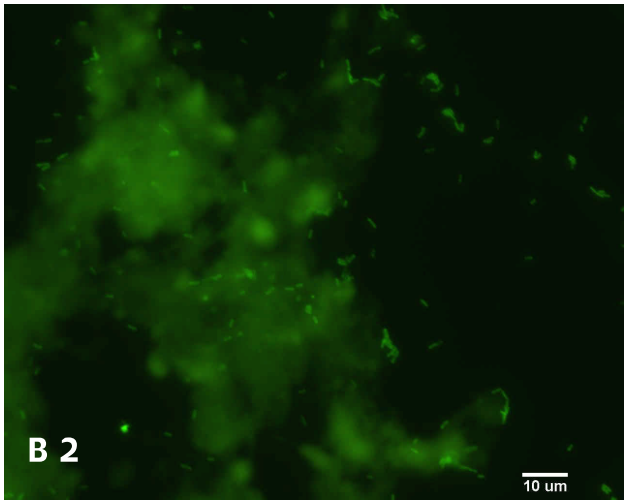


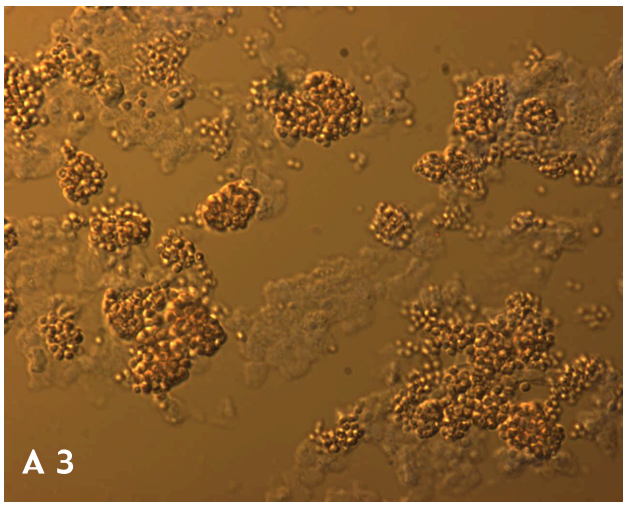
Color Plate 1: Images from the mesohyl of two obligate cryptic sponges. **A:** *Chondrilla sacciformes*, **B:** *Chondrosia* aff. *reniformis*. **A1+B1:** Dapi images of sponge nuclei. **A2+B2:** EUB images of densly packed associated bacteria. Arrows in **B1** and **B2** denote choanocyte chambers. The scale is identical for all pictures.



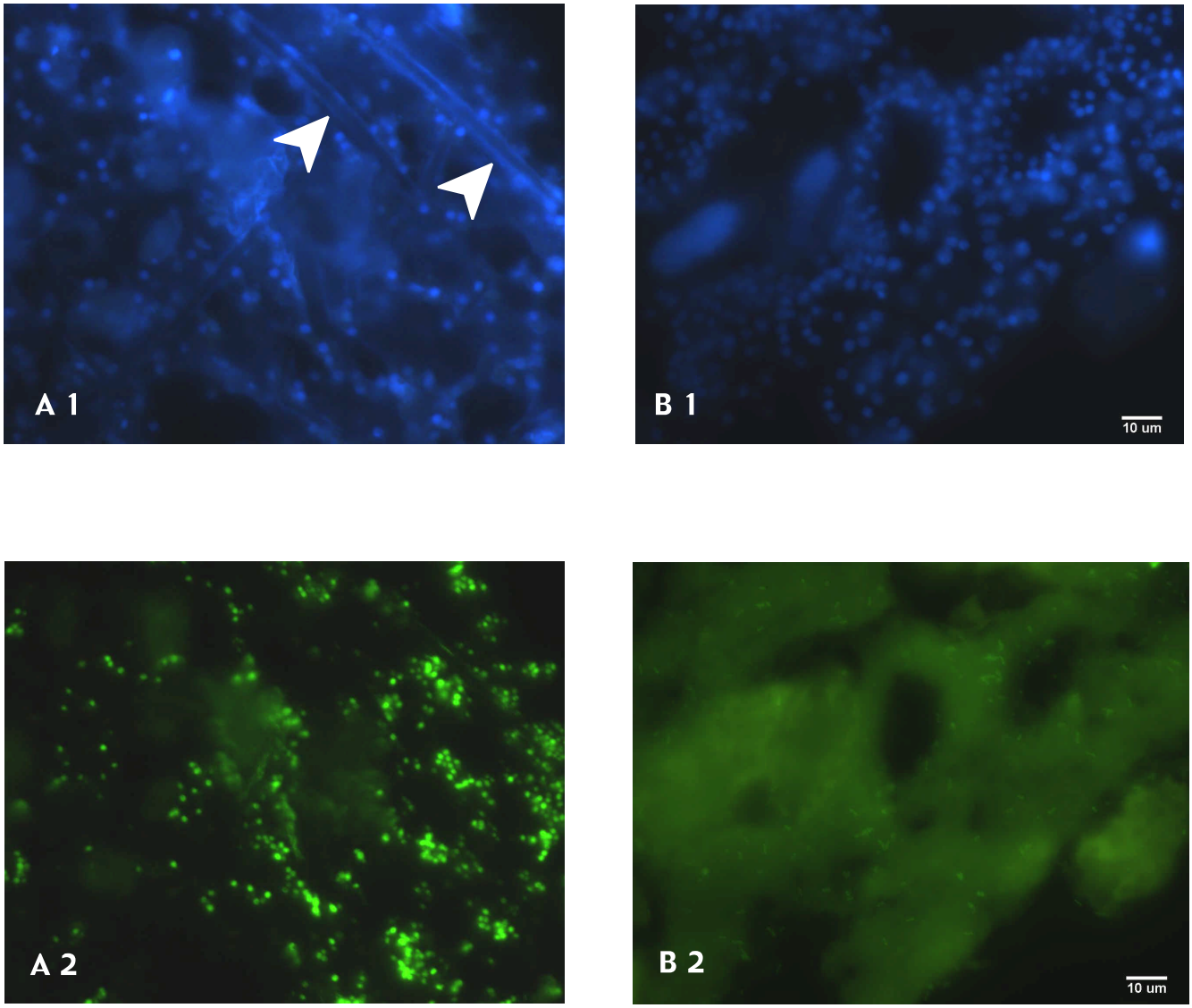








Color Plate 2: Images from the mesohyl of *Hemimycale arabica*, a facultative cryptic species. The individual from series A was collected from a cave, the one from series B from the outer reef surface.
A1+B1: DAPI images of the nuclei of sponge cells, **A2+B2:** EUB images of associated bacteria. Note the sperical cells in A2 packed with bacteria whereas associated bacteria in B2 are loosely scattered over the mesohyl. **A3:** Incident light image of series A. The scale is identical for all pictures.



Color Plate 3: Mesohyl images of two typical epi-reefal sponges. **A:** *Crella cyatophora* , **B:** *Mycale euplectellioides* , **C** is the facultative cryptic *Negombata magnifica*. **A1+B1:** Dapi images of sponge cells, arrow in **A1** denotes spicules and in **B1** choanocyte chambers. **A2, B2+C:** EUB images of associated bacteria. **C:** probably mycelium with attached bacteria breaking it down. The scale is identical for all pictures.